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The series has been investigated thermodynamically by Fuchs (2). The equilibrium diagram is given in Fig. 1. The series consists of a eutectic region from 0 to 82% (by weight) of thallium, and a solid solution phase covering the remainder of the series from its saturation point at 82% thallium to pure thallium.

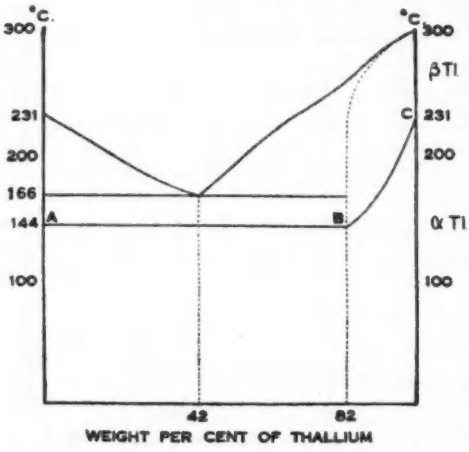

FIG. 1. *Equilibrium diagram for thallium-tin alloys*

In general the superconducting point for an alloy remains constant over a eutectic phase, but in the case of the alloys of thallium and tin marked variations of the type usually associated with solid solutions appear over the whole system. These variations include a cusp at the eutectic point (42% of thallium) and a sharp maximum at the solid solution saturation phase (82% of thallium).

Method

Analysis was carried out by the Hull-Debye-Scherrer powder method using the K_α doublet of molybdenum. The X-ray tube was of the usual Coolidge type with water-cooled target and was operated at 20 to 25 m.a. and 35 to 40 K.V. (R.M.S.). Other radiation than the K_α doublet was removed by the action of a zirconium oxide filter.

The beam was limited by a ½-mm. slit, 3 cm. long. The specimens were mounted directly in front of this slit at the centre of a cylindrical camera of about 9 cm. radius. Exposures of from 25 to 50 hr. were necessary.

The components of each alloy were melted together in Pyrex tubes *in vacuo*. After the melt was complete in the Pyrex tube it was forced through a short fine capillary section of the tube by means of atmospheric pressure. This ensured homogeneity of the alloy.

The powder for analysis was removed from the alloy in question with a fine needle. It was sifted through a 150-mesh sieve and was then sprinkled over part of the surface of a thin glass plate which had previously received a thin coating of flour paste. Powder of a substance of known lattice constant (either copper or tin) was mounted in the same manner on another part of the same glass plate. The plate was then supported so that half of the beam passed through the alloy powder and half through the powder of the substance used for comparison. A septum in the camera kept the two designs from overlapping on the photograph. Thus it was possible to check accurately the radius of the camera for every photograph. In this way lattice constants could be determined to about 0.005 Å.

Comparison photographs were also obtained of the alloys mounted in the form of thin foils, with no supporting glass plate. These photographs showed that no detectable chemical reaction was due to the flour paste, and also indicated that the paste produced no characteristic diffraction lines.

Results

A series of representative photographs is given in Fig. 2. Table I summarizes the readings taken and shows lattice constants obtained.

TABLE I

LATTICE CONSTANTS OF THALLIUM ALLOYS

Thallium, %	Structure	Lattice constant, Å	
0	Double body-centered tetragonal	$a_o = 5.818$	$c = 0.5455$
15	Double body-centered tetragonal Face-centered cubic	$a_o = 5.820 \pm .005$ $a_o = 4.833 \pm .004$	$c = .5455$
35	Double body-centered tetragonal Face-centered cubic	$a_o = 5.822 \pm .006$ $a_o = 4.835 \pm .008$	$c = .5455$
42*	Double body-centered tetragonal Face-centered cubic	$a_o = 5.830 \pm .004$ $a_o = 4.833 \pm .005$	$c = .5455$
58	Double body-centered tetragonal Face-centered cubic	$a_o = 5.824 \pm .006$ $a_o = 4.832 \pm .005$	$c = .5455$
70	Double body-centered tetragonal Face-centered cubic	$a_o = 5.8$ $a_o = 4.837 \pm .003$	$c = .54$
80	Face-centered cubic	$a_o = 4.835 \pm .004$	
90	Face-centered cubic	$a_o = 4.829 \pm .004$	
97	Face-centered cubic Hexagonal close-packed	$a_o = 4.840 \pm .004$ $a_o = 3.45$	 $c = 1.60$
100	Hexagonal close-packed	$a_o = 3.450$	$c = 1.60$

NOTE:—*Radius of camera varied from 9.40 cm. to 9.46 cm. Wave-length of X-rays = 0.710 Å. Probable errors quoted throughout are average deviations.*

**Due to the importance of accuracy in the results obtained for this alloy, four photographs have been taken independently of different specimens of the alloy. The four results agree well among themselves and the above value is an average for the four photographs.*

It was noted that α-thallium, the allotropic form of thallium which is stable at ordinary temperatures and which displays a hexagonal close-packed structure, changes, upon the addition of tin, to β-thallium, which is ordinarily stable only above 231° C. (approximately). Both of these forms correspond to spherical symmetry in the atom, the change being accomplished by a simple gliding of planes. A similar change from α- to β-thallium in the thallium-antimony alloys has previously been noted by Persson and Westgren (3).

The value of the lattice constant obtained for the alloy containing 90% of thallium agrees with that obtained by Sekito (4). The constant of the β-thallium lattice decreases to about 4.833 Å, corresponding to the interposition of the tin atom in the thallium cell. The lattice parameter of thallium-tin alloys containing less than 80% of thallium remains constant at about 4.833 Å throughout the eutectic phase. The constant for tin, on the other hand, undergoes a slight increase in the eutectic phase. This increase has its maximum at or near the eutectic point.

Discussion

In general, the writers' observations on this series of alloys show no marked deviation from the laws describing the structure of alloy systems. However, an unexpected expansion of the tin lattice in the eutectic region has been noted. The value of this expansion is a trifle doubtful since it is not much greater than the experimental errors. It would seem probable that this phenomenon is related in some way to the lowering of the superconducting point. Since no adequate theory has yet been advanced to deal with superconductivity, the writers cannot further support this hypothesis.

The thermodynamic examination mentioned above has revealed another interesting feature of the eutectic region. In the cooling curves of the alloys between 0 and 82% of thallium a second stationary point appears below the point of eutectic crystallization. This stationary point is ascribed by Fuchs to the influence of the presence of tin on the point at which the change occurs from β-thallium to α-thallium. His explanation is strongly supported when he traces the line AB (Fig. 1) which passes through these stationary points, through the solid-solution region to the point C, the point at which the change occurs for pure thallium. We would hence expect to find α-thallium below the line AB, an expectation which is not fulfilled by the X-ray analysis.

The writers would suggest, since the transformation point lies below eutectic crystallization point, that the change which occurs in the thallium atom does not result in a change of crystal structure but succeeds merely in setting up strains resulting in a slight distortion of the tin lattice. This might appear in the form of an increase of the tin-lattice parameter such as has been observed above. Microphotometer traces have been taken which indicate that this distortion, if it exists, is not sufficient to produce a perceptible widening of the X-ray diffraction lines.

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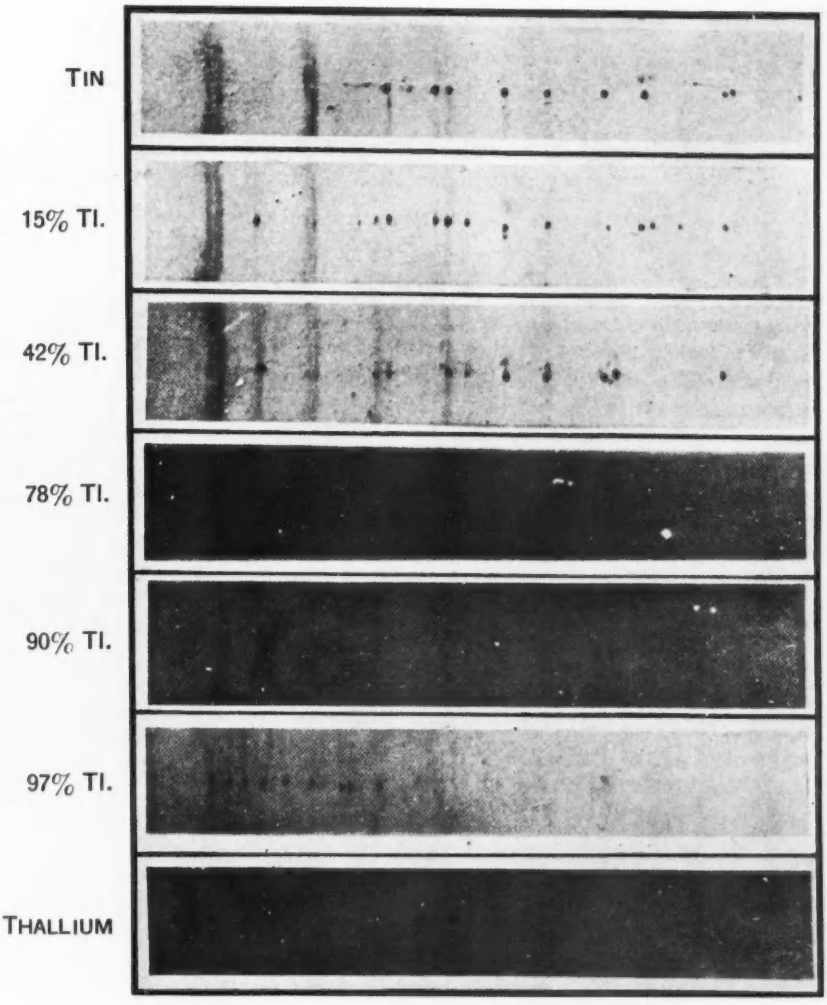

FIG. 2. *Typical Hull-Debye-Scherrer X-ray diffraction spectrograms of thallium-tin alloys.*

THE VAPOR PRESSURE OF VINYL ACETATE[1]

By J. Marsden[2] and A. C. Cuthbertson[3]

Abstract

This paper presents the results of the measurement of the vapor pressure of vinyl acetate, over the temperature range from 0°C. to the normal boiling point. The determinations were carried out on vacuum distilled samples with an isoteniscope, differing slightly in detail from that used by Smith and Menzies(7).

The normal boiling point is 72.5°C. The molecular heat of evaporation has been found to be 8211 calories. The equation which represents the results is

$$\text{Log}_{10}P_{\text{mm.}} = \frac{-0.05223 \times 34433}{T} + 8.091.$$

Trouton's constant and the critical temperature have been found to be 23.8 and 228.3°C.

Experimental

A diagram of the apparatus is shown in Fig. 1. The apparatus was pumped out at *P*. Vinyl acetate* was admitted at *H* by opening a stopcock which was lubricated with glycerol and dextrose. The acetate which contained traces of acetaldehyde and acetic acid was distilled at room temperature into *G* which was suitably cooled with an ice-salt mixture. When the appropriate amount had distilled over, the tap connecting *G* and *H* was closed. On warming *G* and cooling *E*, a sample was distilled into the isoteniscope. A sufficient quantity was distilled to fill the apparatus including the carboy *C*, with vapor at a few centimetres pressure. The isoteniscope was then sealed off from the distilling apparatus. The limbs of the isoteniscope were about two-thirds full of liquid. The liquid was brought to constant temperature, accurate control of which was aided by brisk stirring and felt insulation on the water bath. On connecting the apparatus through the two-way stopcock *P* to the pump, the liquid began to boil in the bulb *F*. It was found however that without a capillary tube attached as shown at *F*

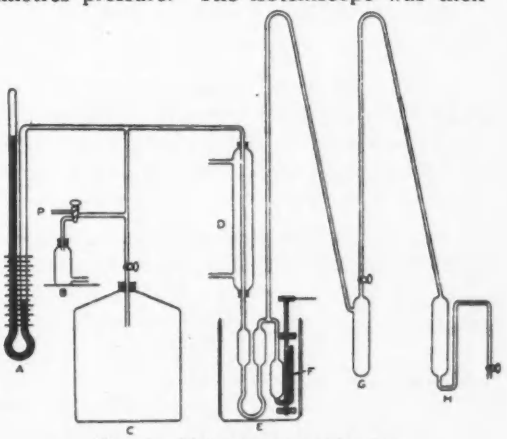

Fig. 1. *Vapor pressure apparatus.*

[1] *Manuscript received May 11, 1933.*
Contribution from the Department of Chemistry, Mount Allison University, Sackville, New Brunswick, Canada.
[2] *Instructor in Chemistry, Mount Allison University.*
[3] *Assistant Professor of Chemistry, Mount Allison University.*
* *Kindly supplied by Shawinigan Chemicals Co.*

vaporization took place without ebullition. With the capillary however the surface was continually broken,—a necessary precaution to ensure equilibrium being established between liquid and vapor. In order to reduce loss during the boiling of the liquid, a reflux condenser *D* was added.

The vapor pressure was determined by connecting the apparatus to *B* and allowing dry air to enter slowly through a fine capillary which was attached to the lower end of the drying bottle. When the height of the liquid in

TABLE I

VAPOR PRESSURE VALUES OF VINYL ACETATE

Temp., °C.	Press., cm.	Log press.	$1/T \times 10^3$	Temp., °C.	Press., cm.	Log press.	$1/T \times 10^3$
−0.15	3.19	.5032	3.665	38.50	20.69	1.3155	3.210
3.65	3.79	.5780	3.615	40.05	22.07	1.3438	3.195
5.23	4.02	.6042	3.595	42.17	24.07	1.3813	3.173
7.80	4.63	.6656	3.562	44.23	26.15	1.4190	3.152
10.70	5.44	.7353	3.531	46.49	28.72	1.4578	3.130
13.15	6.25	.7961	3.495	48.42	31.73	1.5014	3.112
15.93	7.18	.8561	3.462	51.64	35.13	1.5417	3.080
19.15	8.63	.9360	3.422	55.62	41.07	1.6135	3.043
21.07	9.46	.9759	3.401	57.20	43.94	1.6429	3.028
23.05	10.59	1.0249	3.378	59.00	46.96	1.6717	3.012
25.30	11.50	1.0607	3.352	61.32	50.97	1.7073	2.991
27.30	12.69	1.1033	3.330	64.25	56.74	1.7539	2.965
28.90	13.68	1.1360	3.312	66.62	61.73	1.7905	2.944
31.62	15.24	1.1829	3.283	68.90	66.63	1.8237	2.925
32.21	15.90	1.2011	3.277	72.10	74.37	1.8714	2.898
33.42	16.53	1.2183	3.263	72.50	76.00	1.8808	2.895
36.94	19.33	1.2862	3.225				

the two arms of the isoteniscope was level, the manometer reading gave the vapor pressure for a given temperature. The carboy *C* had a capacity of 51 litres which was sufficiently large to prevent sudden pressure changes and permitted the accurate control of the liquid movement in the limbs of the isoteniscope. The values obtained for the vapor pressure are given in Table I. The logarithms of the pressures and the reciprocals of the absolute temperatures are also included.

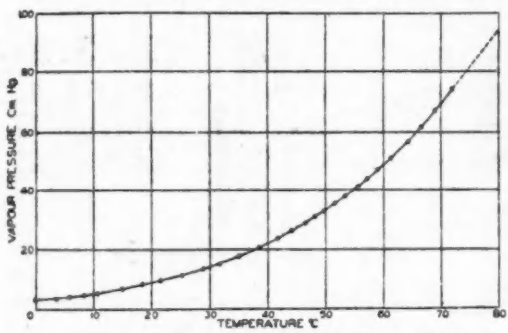

FIG. 2. *Vapor pressure of vinyl acetate from 0° to 80°C.*

The relation between pressure and temperature was plotted and is shown in Fig. 2.

On plotting the logarithm of the vapor pressure against the reciprocal of the absolute

temperature a straight line was obtained which permitted the calculation of the latent heat of evaporation and Trouton's constant. The equation which represents the results as plotted in Fig. 3 is

$$\text{Log}_{10}P_{\text{mm.}} = \frac{-0.05223 \times 34433}{T} + 8.091.$$

The value of the molecular heat of evaporation obtained from the slope of the line was found to be 8211 calories. Trouton's constant was calculated as 23.8.

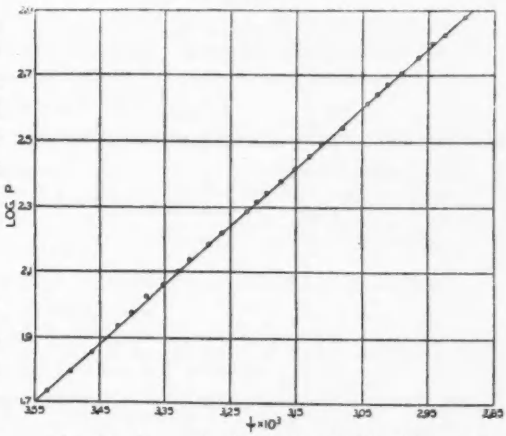

FIG. 3. *Curve showing proportionality between the logarithm of the vapor pressure and the reciprocal of the absolute temperature.*

The Calculation of the Critical Temperature

In an attempt to get an approximate value for the critical temperature of vinyl acetate three methods have been employed and the average of the values calculated was taken as most representative.

Ramsay and Shields (5) give the following relation between critical temperature and surface tension;

$$\gamma \left(\frac{M}{d}\right)^{\frac{1}{3}} = k\,(t_c - t - 6),$$

where γ = surface tension; M = molecular weight; d = density at temperature t, and t_c = critical temperature. Using the surface tension values of Green, Marsden and Cuthbertson (1) at 20, 25 and 30°C. the average value for t_c was 228.9°C.

Ramsay and Young (6) pointed out that if the absolute boiling points of two closely related liquids A and B are compared under equal pressures the following relation will be found to hold,

$$\frac{T_A'}{T_B'} = \frac{T_A}{T_B} + c\,(T_A' - T_A)$$

where T_A and T_B are the absolute boiling points of two similar liquids and T_A' and T_B' are the absolute critical temperatures of the liquids. The constant has been taken as zero.

Two liquids, ethyl propionate and normal propyl acetate, have been chosen as similar liquids. They have five carbon atoms in the molecule and the value of the Ramsay and Shields constant is 2.3.

TABLE II

CRITICAL TEMPERATURES AND BOILING POINTS OF ETHYL PROPIONATE AND NORMAL PROPYL ACETATE

—	Critical temp., °C.	B.p., °C.
Ethyl propionate	272.9	99.10
Normal propyl acetate	276.2	101.7

Values for the critical temperatures and boiling points of these two compounds, taken from the International Critical Tables (2, p. 248) are given in Table II.

The critical temperature of vinyl acetate calculated from these data is 233.6°C.

Sugden (8) has shown that the equation $D-d=D_0\left(1-\frac{T}{T_c}\right)^{\frac{3}{10}}$ is trustworthy for the relation between density and temperature of unassociated liquids; where D = density of the liquid at absolute temperature T; d = density of the vapor; $D_0=\frac{M}{V_0}$, where M = molecular weight and V_0 = molecular volume at absolute zero. T_c is the absolute critical temperature. The zero volume may be calculated from atomic and structural constants. For vinyl acetate the value is 70.6. The values obtained at 10° and 30°C. give an average value of 222.4 for the critical temperature. The values calculated by the various methods are shown in Table III.

TABLE III

CALCULATED CRITICAL TEMPERATURES

Method of calculation	Critical temp., °C.
Ramsay and Shields	228.9
Ramsay and Young	233.6
Sugden (zero volume)	222.4
Average	228.3

Discussion of Results

In order to check the vapor pressure curve, the boiling point of air-distilled vinyl acetate was determined. At a corrected pressure of 74.35 cm. the liquid boiled at 72.2°C. The value as read from the vapor pressure-temperature curve (Fig. 2) is 72.25°C.

It would seem probable that, owing to polymerization, the vapor pressures of vinyl acetate at elevated temperatures would be considerably lower than those of the monomer. If this were so the value of the vapor pressure should be a function of the time of heating at higher temperatures. In order to check this possibility a fresh sample distilled *in vacuo* was raised to a temperature of 70°C. in 15 min. The value obtained agreed accurately with those obtained in the normal course of measurements which extended over two hours. Polymerization then appeared to be so slight that it had no perceptible influence on the vapor pressure. However, if samples stand in contact with air, a pronounced effect is noted. This effect can be accentuated by

bubbling oxygen through the liquid. One finds a marked increase in viscosity which is a sensitive criterion of polymerization. Care was taken to exclude oxygen from the isoteniscope, which probably accounts for the negligible effects produced at elevated temperatures.

The value of Trouton's constant (23.8 as compared to an average normal value of 21.7) might suggest an associated liquid. It was found that Ramsay and Shields' constant of 2.41 is higher than the accepted average value of 2.12 (1). It is notable that some acetates (3, p. 450; 4, p. 136) show about the same divergence for both constants.

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THE ACTION OF CARBON DISULPHIDE ON ALUMINA GEL[1]

By L. A. Munro[2] and J. W. McCubbin[3]

Abstract

The authors have investigated the yellow color observed when carbon disulphide was adsorbed by c.p. alumina at room temperature. The color is due to by-products of the reactions of carbon disulphide with residual water in the gel. The investigators of the $CS_2 + H_2O$ reaction at higher temperature attribute the yellow to sulphur or aluminium sulphide. The color formed at room temperature is not due to either of these. The reaction products consist largely of hydrogen sulphide, water, and carbon dioxide, with small amounts of carbonyl sulphide and carbon monoxide. The yellow coloration has been found to be a mixture of sodium sulphide, sodium hydrosulphide, and sodium polysulphide. A mechanism is proposed for its formation.

Introduction

During experiments on the adsorption of various vapors by alumina gel (13), the formation of a yellow color on the sorbent was noticed when carbon sulphide was used. This color could not be removed with the usual solvents for sulphur.

No references to the formation of a yellow coloration with carbon disulphide at room temperature, using alumina or any other sorbent, were found in the literature. Gurwitsch (6) mentions the evolution of hydrogen sulphide when carbon disulphide is adsorbed by fibrous alumina. He does not state the temperature at which this reaction was observed, the experimental technique, nor his method of analysis of the reaction products. No yellow coloration is recorded.

Simonin (17) and Allmand and Lizius (1) have measured the sorption of carbon disulphide by active charcoal at room temperature. They did not report any yellow deposit.

Various investigators have noted a yellow coloration at higher temperatures (2, 5, 14, 15). It has been shown that sulphur is formed at higher temperatures with some catalysts.

The present study was undertaken to ascertain the nature of the yellow coloration produced at room temperature, and the reactions by which it is formed.

Experimental and Discussion

The Gel

Mallinckrodt's alumina gel was used in the original sorption study (13). Baker's product and that of the British Drug Houses also gave the yellow coloration. Both are doubtless prepared from bauxite.

A sample of prepared gel was also investigated. It was obtained by precipitation from a hot solution of aluminium nitrate with ammonium hydroxide. It was thoroughly washed and dried at 25° C. to a hard glass-like mass.

[1] *Original manuscript received June 26, 1933.*
Contribution from the Department of Chemistry, Queen's University, Kingston, Ont. Presented to the Royal Society of Canada, May, 1933.
[2] *Assistant Professor of Chemistry, Queen's University, Kingston, Ont.*
[3] *Demonstrator, Department of Chemistry, Queen's University.*

A careful analysis of Baker's gel gave the following figures:—water, 35.3%; silica and ferric oxide, traces; alkali metals, 0.06%; and the remainder, alumina. The analysis for the alkali metals was made according to the method outlined by Washington (20). As the amount was approximately equal to the experimental error involved in his method, qualitative microchemical tests were tried on a hot-water extract of the gel in platinum. These tests revealed the presence of sodium, which was combined with the hydroxyl radical. This was confirmed by a spectroscopic analysis, using a copper arc free from alkali.

Along with the lines from the copper arc and the bright ones of aluminium, faint lines for sodium and also fainter ones for calcium, magnesium, silicon, and iron were visible. Potassium was shown to be absent. Baker's gel was chosen as the catalyst in this investigation.

Activation of the Catalyst

Munro and Johnson (13) showed that the optimum temperature of activation for the sorption of ether vapor was 400° C., which left a residue of 4.5–7.2% of water in the gel. This temperature was confirmed by Chowdhury and Bagchi (3) as the optimum for the removal of sulphur compounds from oil by alumina gel. Therefore, 400° C. was chosen as the activation temperature in this study.

Purification

The c.p. carbon disulphide was purified by very slow reflux distillation through phosphorus pentoxide in an all-glass apparatus. Only the middle fraction was employed. This was redistilled just before use and kept over mercury. It had the characteristic sweet ethereal odor of pure carbon disulphide.

That the purified carbon disulphide was free from hydrogen sulphide was shown by different experiments. Nitrogen saturated with carbon disulphide was bubbled through a copper acetate solution for 48 hr. and there was no precipitation of copper sulphide. In a second experiment the carbon disulphide was bubbled through iodine solution for some time. There was no difference in the titrations before and after contact with carbon disulphide.

Experimental Methods

Dry carbon dioxide-free air was passed through a saturator of carbon disulphide and through the activated alumina. The saturator and the alumina were kept in an air bath at 25° C. Each experiment was stopped when the alumina tube had completely assumed the canary yellow color.

To make sure that the formation of the color was not due to oxidation, nitrogen, purified with pyrogallol made up according to the directions of Wolf and Krause (21), was used during activation and as carrier during sorption. There appeared to be no difference in the reaction, the yellow color appearing as usual.

Photochemical effects were also eliminated by carrying out distillation, activation, and sorption in the dark. The reaction proceeded as before.

Identification of the Reaction Products

It was found early in the course of the work that hydrogen sulphide was given off as one of the reaction products. The only hydrogen present was that contained as water in the residual water in the gel. The conclusion was that this must be a reaction involving carbon disulphide and water, with perhaps a subsequent reaction with some impurity in the gel.

From the work of Neumann and Altmann (14), Stock, Siecke and Pohland (19) and others, it appeared that the reactions might result in the possible formation of carbon disulphide, carbon dioxide, carbonyl sulphide, carbon monoxide, carbon sulphide, hydrogen sulphide, water, sulphur dioxide and sulphur. A quantitative determination of the products was not necessary for the elucidation of a mechanism of the reactions, but rather identification of all the products. This was undertaken.

There is no method of analysis outlined in the literature for such a mixture. The methods given for smaller mixtures are vitiated by the presence of certain components of the larger mixture. Further, the methods given are for static determinations and could not be used dynamically without modification. An account of the examination of the possible reaction products, together with the conclusions drawn, are given below.

Sulphur. The fact that the yellow color was not removed by solvents for sulphur precludes the presence of free sulphur unless in an insoluble modification. As the reaction takes place at room temperature this seemed highly improbable.

Hydrogen Sulphide and Sulphur Dioxide. It was observed early in the investigation that the formation of the yellow color was accompanied by the evolution of hydrogen sulphide. For the detection of sulphur dioxide, the sulphide was completely precipitated by bubbling the exit gases through cadmium acetate solution and the filtrate tested for sulphur dioxide with fuschin. Negative results were obtained. Sulphur dioxide was also absent in the desorbed gases.

After proof of the absence of sulphur dioxide, hydrogen sulphide was shown to be present in large amounts by means of an iodine solution in potassium iodide. Carbonyl sulphide does not react with this reagent. With the salt of a heavy metal, however, it gradually precipitates the sulphide.

Carbon Dioxide. Carbon dioxide could not be identified by the usual methods owing to the interference by carbon disulphide and carbonyl sulphide which react with alkali with the formation of carbonates and thiocarbonates. Identification can be made by taking advantage of the considerable difference in rates of absorption of these gases or vapors in alkali of different concentrations. Stock and Seelig (18, p. 676) give the following method for the analysis of a mixture of carbon monoxide, carbon dioxide, carbonyl sulphide and carbon disulphide:—*(a)* Sodium hydroxide (1 cc. of 30%) is introduced into the burette. The volume is read each minute for several minutes. A rapid shrinkage shows the presence of carbon dioxide. *(b)* Water (4 cc.)

is added, and the volume read every 10 min. for one hour (carbonyl sulphide determination). *(c)* Potassium hydroxide (1 cc. of 30%) is added and the volume recorded after one, two and three days (carbon disulphide determination). *(d)* The residual gas (carbon monoxide) is determined by cuprous chloride.

After the removal of hydrogen sulphide the remaining products, with the exception of carbon monoxide, were condensed in liquid air and examined by the above method. An immediate rapid shrinkage in volume was noted. This could only be carbon dioxide.

Carbonyl Sulphide. Fig. 1 shows the absorption curves for *(b)*, for two different experiments. The absorption of carbon disulphide from a saturated air-carbon disulphide mixture is shown in curve No. 3. It will be seen that in approximately one hour the rates in curves Nos. 1 and 2 become similar to that of No. 3. From these and other experiments it was concluded that some carbonyl sulphide was present in the reaction products.

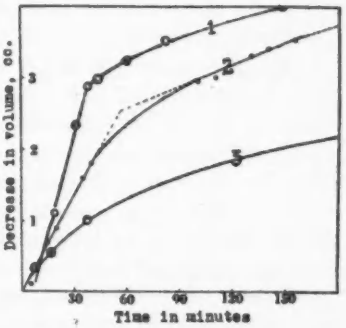

FIG. 1. *Rate of absorption by 6% sodium hydroxide. Curves 1 and 2. Condensates by liquid air. Curve 3. Carbon disulphide from saturated air mixture.*

Carbon Disulphide. Carbon disulphide was always present as the result of incomplete reaction.

Carbon Monosulphide. The existence of gaseous carbon monosulphide has been questioned although the brown polymer is known (9). Lewis and Lacey (10) suspected its formation in their investigation of the equilibrium $CO+S \rightarrow COS$, but they did nothing to confirm this. The writers have found no evidence of either form in the reaction products.

Carbon Monoxide. Any carbon monoxide formed would pass through the liquid-air trap. The residual gases were analyzed for carbon monoxide in a Fisher Universal gas analysis apparatus. The carbon monoxide was passed over heated copper oxide and the carbon dioxide absorbed in caustic. Carbon monoxide was found to be present in small amounts.

Water. It was found that under ordinary conditions water was absent from the exit gases, owing to adsorption by the active gel. It was detected in the reaction products after reaction had gone on for some time, or when the activation temperature was lowered to 150° C.

Identification of the Yellow Coloration

It has been shown above that the yellow coloration is not sulphur in its ordinary form. Neumann and Altmann (14) suggest that, during the reaction of carbon disulphide on water vapor in the presence of alumina, aluminium sulphide is formed as an intermediate, and is then hydrolyzed by the water to form alumina and hydrogen sulphide. Accordingly, if water were used to

extract the gel, the yellow color would disappear owing to the reaction stated above. This was tried on the yellow gel, and contrary to expectations, although the gel became white, the aqueous extract was a clear yellow.

Qualitative analysis by micro methods showed that this solution contained sodium combined with sulphide, hydrosulphide and some polysulphide. The sodium was detected by the formation of the characteristic tetrahedra and octahedra of sodium uranyl acetate. After boiling for 10 min. hydrogen sulphide was still present in the vapor, indicating the hydrolysis of a hydrosulphide. The test of Rule and Thomas (16) for sodium disulphide was positive.

The gummy residue, left on evaporation of the water extract of the yellow coloring matter in a stream of nitrogen, revealed the bright sodium doublet 3302.5 and 3302.94 Å, as well as the very sensitive magnesium line 2852.12 Å. However a negative test for magnesium (sensitivity 1/100,000) as outlined by Feigl (4, p. 245) showed that it was present in traces only.

From the foregoing it is concluded that the following products are formed in the reaction: hydrogen sulphide—in the largest quantities—water, carbon dioxide, and small amounts of carbonyl sulphide and carbon monoxide. The gel contains as a yellow coloration a mixture of sodium sulphide, sodium hydrosulphide and a small amount of sodium polysulphide.

Proposed Mechanism of the Reactions

The primary reaction is one between carbon disulphide and water. These may react in two ways,

$$CS_2 + 2H_2O \rightarrow CO_2 + 2H_2S. \quad (1)$$

$$CS_2 + H_2O \rightarrow COS + H_2S. \quad (2)$$

According to Neumann and Altmann (14) reaction No. 2 seems to predominate at lower temperatures. A sufficient number of thermochemical data are not available to determine by that means which of these two reactions will predominate at room temperature.

Carbonyl sulphide reacts with water according to the equation:

$$COS + H_2O \rightarrow CO_2 + H_2S. \quad (3)$$

Stock and Seelig (18) have studied the decomposition of carbonyl sulphide, and they state that it breaks up according to the equation

$$COS \rightarrow CO + S. \quad (4)$$

The investigation of Lochte-Holtgreven and Bawn (11) on the structure and decomposition of carbonyl sulphide led them to believe that the sulphur formed in this decomposition (No. 4) is an excited sulphur atom with excitation energy of 35 cal. Although there was no investigation into the reactivity of this sulphur, it might be that it would combine much more readily with a sulphide to form a polysulphide.

Analysis has shown that there is a trace of sodium hydroxide in the gel. The hydrogen sulphide reacts with this to form sodium hydrosulphide:

$$NaOH + H_2S \rightarrow NaHS + H_2O. \quad (5)$$

The sulphur from the decomposition of carbonyl sulphide may now react with the sodium hydrosulphide to form the polysulphide.

$$2NaHS + S \rightarrow Na_2S_2 + H_2S. \qquad (6)$$

It will be seen from this that hydrogen sulphide is produced in the largest quantities. The writers found the same to be true experimentally.

Further Investigation to Support Proposed Mechanism

To see whether the yellow coloration was being caused as the result of a secondary reaction between the hydrogen sulphide and the trace of alkali in the gel, dry hydrogen sulphide was passed through activated alumina at room temperature. A calcium chloride tube was placed directly after the alumina to detect the presence of water formed in the reaction.

The yellow color formed in the tube as before, but with a gradation from an intense yellow at the entrance end to white at the exit end. As shown by equation No. 5 water is given off as the result of the reaction. Some of this water formed is taken up by the alumina, preventing adsorption of the hydrogen sulphide, and therefore preventing the reaction in which the yellow coloring matter is formed. After saturation the water emerged and was absorbed by the calcium chloride. These results are recorded in Table I.

TABLE I

SORPTION OF HYDROGEN SULPHIDE

Vol. of H_2S supplied, S.T.P., cc.	165	235	375	540	627
Weight of H_2S supplied, gm.	0.2504	0.3567	0.5692	0.8197	0.9513
Gain in weight of Al_2O_3, gm.	0.1304	0.1963	0.3235	0.4505	0.4741
Gain in wt. of $CaCl_2$, *i.e.*, loss of water from gel	Nil	Nil	Nil	0.0020	0.0063

NOTE:—*Adsorbent, 17.240 gm.; residual water, 7.0%; activation temp., 375° C.*

Carbonyl sulphide reacts with sodium hydroxide, but the reaction is rather slow. It also reacts very slowly with water to form hydrogen sulphide and since, according to the proposed mechanism, the formation of the yellow color depends on the initial production of hydrogen sulphide, it was decided to investigate the action of pure carbonyl sulphide on the active alumina.

Carbonyl sulphide was prepared by the action of dilute sulphuric acid on potassium thiocyanate (8). It was purified by bubbling through 30% sodium hydroxide, iodine solution, then through a condensing worm immersed in solid carbon dioxide and chloroform, and thence through the alumina. A faint coloration appeared throughout the gel.

This is what would be expected from equation No. 3. It may be concluded that this reaction goes to a very slight degree at room temperature. However, on standing for some time the gel became much more yellow, with the evolution of hydrogen sulphide.

Purification of the Gel

It was thought that the sodium hydroxide in the gel might be removed by electrodialysis. A modified form of the dialysis cell as described by Holmes (7) was used. Mechanical stirring proved to be much more efficient than the compressed air method described by Holmes. Heat was supplied to the cell by means of a lamp enclosed in an asbestos box under the cell. Platinum gauze electrodes were substituted for the carbon ones recommended. A potential of 110 volts was used.

A drop from 20 to 0.6 milliamperes occurred in the first two days, and thereafter the current remained constant at the low amperage. The dialysis was continued for six weeks and the gel was then removed. Even after this time the gel gave the same coloration after reaction with carbon disulphide.

Regarding the removal of the electrolytes from gels, Lottermoser (12) states, "Absolutely electrolyte-free, pure silica sol cannot be prepared."

Use of Extracted Gel

Gel that had been saturated with carbon disulphide was washed thoroughly with distilled water, dried at 110° C., and reactivated at 400° C. The residual water in the original sorbent was 9.2%; in the reactivated gel 9.9%. On passing carbon disulphide vapor through this gel no coloration developed, but hydrogen sulphide was given off. Sorption curves are shown in Fig. 2. The aqueous extract of this saturated gel gave no microchemical test for sodium. This fact supports the proposed mechanism.

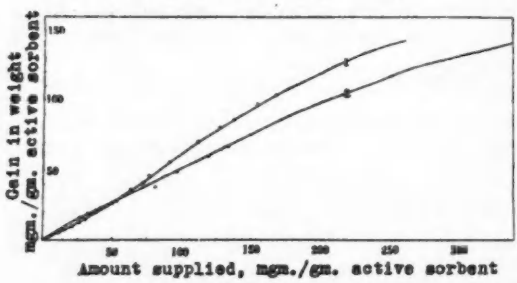

FIG. 2. *Sorption by original and extracted gels. Curve 1. Sorption by original gel. Curve 2. Sorption by gel after extraction of yellow color and reactivation.*

Acknowledgments

The authors wish to acknowledge their indebtedness to Queen's University for an assistantship to one of them (J. W. M.); and to the departments which helped with spectrum analysis and photography.

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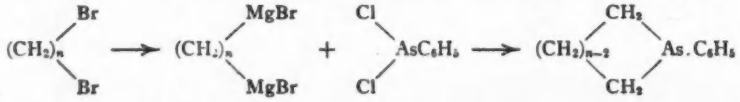
STUDIES ON SOME UNSYMMETRICAL TETRAMETHYLENE GLYCOLS[1]

By C. F. H. Allen[2], C. V. Wilson[3] and W. L. Ball[3]

Abstract

As intermediates for obtaining unsymmetrical 1, 4-dibromides several tetramethylene glycols have been prepared, using varied procedures. They are not tractable substances. Only one gave a dibromide that could be purified; the latter did not form a Grignard reagent when treated with magnesium in dry ether. Trimethylene chlorobromide gives a small amount of Grignard reagent.

Heterocyclic compounds in which one of the atoms forming a part of the ring is arsenic have been prepared through the Grignard reaction (4, 5, 11).



The writers wished to study some of these heterocyclic compounds that were unsymmetrical, the preparation of which would require branched chain dibromides; only one of the latter was found in the literature (6, 13). The corresponding glycol, β-methylbutanediol-1,4, was previously known (6), but the necessary reactions were tedious and slow, and the yield low, considering the expensive starting material. A cheaper method was devised but the final yield was no better: citric acid → itaconic acid → methylsuccinic acid → methyl succinic ester → β-methylbutanediol.

β-Phenylbutanediol-1,4 was obtained by a sodium-absolute alcohol reduction of phenylsuccinic methyl and ethyl esters. While this work was in progress, Manske (7) described this glycol, prepared by an almost identical procedure, as an oil. In the writers' experiments a monosodium glycolate was always isolated and on acidification, the glycol was obtained as a crystalline solid. A homologue, β-(2,4-dimethoxyphenyl)-butanediol-1,4, was made by a similar reduction of the corresponding succinic ester.

Only the β-methylated glycol gave a dibromide that could be obtained in a pure state; the tendency to dehydration or removal of hydrogen bromide was very marked, the only derivative of the dimethoxyglycol that could be prepared being a diacetate. β-Methyltetramethylenedibromide-1,4 reacted with magnesium with formation of magnesium bromide, but if any Grignard reagent was formed the amount was too small to be detected.

A quantitative study of the formation of Grignard reagents from dihalides has not yet been made, but based on yields of products actually obtained, the tetra- and pentamethylene dibromides must have given 25–40% (4, 5,

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Contribution from the Department of Chemistry, McGill University, Montreal, Canada.
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11, 13, 14). The trimethylene gave under 1% (15) and ethylene dibromide and magnesium are said to yield ethylene "exclusively". It was thought that by using trimethylene chlorobromide the less reactive chlorine might allow the formation of a Grignard reagent, although not enough was obtained from ethylene chlorobromide to give Gilman's color test (3). A positive result was obtained, but the yield of Grignard reagent was too low to be practical (8%). This suggests that better yields might be obtained with higher mixed dihalides.

Experimental

β-Phenylbutanediol-1,4. This reduction was carried out essentially according to the published procedure, but the process of isolation differed. After refluxing had been completed, 300 cc. of water was added and the bulk of the alcohol distilled through a short column; when the temperature of the vapor reached 95° C. the heating was stopped. If allowed to stand overnight, flaky crystals separated, but as these were extremely difficult to filter, benzene was added and the lower layer drawn off; the solid that separated between the two layers was easily filtered. This substance is a sodium salt of the glycol and absorbs carbon dioxide rapidly. On acidification and extraction of the solution with benzene, followed by drying and distillation, the glycol was readily obtained as an oil (b.p. 158–60° C. at 8 mm.) which crystallized on cooling. After recrystallization from benzene or ether-petroleum ether it formed hexagonal plates, m.p. 70° C. Usually, to save time, the residual solution after removal of the alcohol was acidified at once and the oil taken up in benzene. The latter was shaken with sodium carbonate solution to remove a little phenyl succinic acid, then dried and distilled. The first crystalline material did not separate for several weeks, but once available for seeding, all the oils could be crystallized. The yield of sodium salt was 30 gm. from 62.5 gm. of ester, which gave 16–18 gm. of glycol (40–45%). The oily residues were combined and worked up for more glycol. The yield was not increased by using the methyl ester or substituting butyl alcohol. The sodium salt is a hygroscopic white solid, that absorbs carbon dioxide rapidly. Analysis:—Calcd. for $C_{11}H_{13}O_2Na.C_2H_6O$: Na, 9.8%. Found: Na, 9.6, 9.7%.

The bis-phenylurethane was prepared in the usual manner; it melted at 114° C. and a mixed melting point with an authentic specimen was not depressed*. The dibromide was never obtained in a pure state. Several procedures were employed including Manske's, but in every case an oil (b.p. 130–168° C. at 8 mm.) resulted. It was acid to litmus, liberated gas with methyl magnesium iodide, and contained 35% bromine (calcd., 54.8% Br). Obviously, it was unsuited for making a Grignard reagent.

β-(2,4-Dimethoxyphenyl)butanediol-1,4. This glycol was also prepared by a sodium-alcohol reduction of the corresponding ester. The latter was obtained in a yield of 80% by refluxing for 10 hr. a mixture of 90 gm. of the

**This substance had been prepared by Dr. Manske, and the authors are indebted to him for the mixed melting point determination.*

corresponding anhydride (from resorcinol dimethyl ether*, maleic anhydride and anhydrous aluminium chloride (9)), 200 gm. of methyl alcohol and 48 gm. of concentrated sulphuric acid, and distilling *in vacuo* (m.p., 62° C.). The reduction was carried out in the usual manner. After removal of the excess alcohol, benzene was added. On cooling, the glycol often crystallized. It separated from ether in fine prisms: m.p. 89° C.; yield, 50%. Analysis:—Calcd. for $C_{12}H_{18}O_4$: C, 63.7; H, 7.9; OCH_3, 27.4%; mol. wt. 226. Found: C, 63.9; H, 8.0; OCH_3, 27.5; mol. wt., 216.

This glycol† did not form a single solid derivative; it lost water on treatment with phenyl and α-naphthyl isocyanates, *p*-chlorobenzoyl and 3,5-dinitrobenzoyl chlorides, and was recovered unchanged after treatment with trityl chloride in pyridine. It gave a liquid diacetate with acetyl chloride: 9 gm. of the glycol was dissolved in 20 cc. of acetyl chloride; hydrogen chloride was copiously evolved. The excess solvent was allowed to evaporate and the residue taken up in benzene, dried with calcium chloride and distilled *in vacuo;* 10 gm. of the ester (b.p. 221–4° C. at 18 mm.) was obtained. Analysis:—0.5525 gm. gave 0.2152 gm. $C_2H_3O_2$. Calcd., 0.2140 gm. On hydrolysis the glycol was regenerated.

No dibromide could be prepared by any method; the crude oil from various attempts analyzed 36.6% Br (calcd., 45.5%) but lost hydrogen bromide spontaneously. It boiled from 60–140° C. at 5 mm. and the distillate contained only 8% Br.

β-Methylbutanediol-1,4. This glycol was prepared by the reduction of methyl succinic ester using butyl alcohol and sodium. After the addition of water the mixture was cooled and carefully neutralized with hydrochloric acid, the upper layer separated and the butyl alcohol distilled *in vacuo*. The residue from a run using 38 gm. of ester was extracted with ether and after removal of the solvent was distilled (b.p. 112–4° C. at 10 mm.), but when redistilled at 8 mm. gave two fractions: (*a*) 6 gm. (26%), b.p. 100–110° C. which was mainly the desired glycol; and (*b*) b.p. 135° C.; the refractive index of the latter was 1.4322^{20}_{D}. The refractive index of 2-methyl-2-butene-1,4-diol (b.p. 128° C. at 7 mm.) is 1.4815^{20}_{D} (10). From the first a bis-phenylurethane was prepared, having a melting point 99–100° C. (6).

The dibromide was prepared as directed by Harries (6), but the yield claimed could not be duplicated, nor was any better result obtained by other procedures; from 10 gm. of glycol was obtained 4–6 gm. of dibromide. The latter did not react with magnesium in dry ether without a crystal of iodine or Gilman's catalyst (2). After refluxing for 2.5 hr. much of the metal was unacted upon. White crystals of magnesium bromide etherate (8, 12) separated. Gilman's color test (3) was negative. No acid was produced on carbonation, nor could a mercuri-halide be prepared.

**A liberal sample of this was kindly donated by E. I. DuPont de Nemours Co.*

†When it was treated with p-chlorbenzoylchloride in pyridine, a white solid m.p. 195–96° C. resulted, which on analysis gave 24.1% chlorine. It was found to be p-chlorbenzoic anhydride (calcd. for $C_{14}H_8O_3Cl_2$: Cl, 24.1%), yielding p-chlorbenzoic acid quantitatively on hydrolysis. The glycol was recovered unchanged.

Bromobutyl acetate. An attempt to form a dibromide from butyleneglycol diacetate ($\begin{pmatrix}CH_3CHOCOCH_3\\ |\\ CH_2CH_2OCOCH_3\end{pmatrix}$) was unsuccessful, only one bromine being introduced. Butylene glycol diacetate* (50 gm.) was saturated with hydrogen bromide (50 gm. increase in weight) and after several hours poured upon cracked ice. The oil was extracted with ether, purified in the usual manner and dried over potassium carbonate. It gave a colorless liquid on vacuum distillation (b.p. 92–4° C. at 27 mm.). Analysis:—Calcd. for $C_6H_{14}O_2$ Br: Br, 41.0%. Found: Br, 40.7, 41.2%. The ester was recovered unchanged after again saturating with hydrogen bromide; the location of the bromine was not determined.

In view of the recent success in reduction of esters to alcohols at very high pressures, using a copper-chromite catalyst (1), it was hoped that the glycols could be produced in this manner in a much better yield. Unfortunately the reaction proceeded too far, resulting mainly in a branched chain primary alcohol or cleavage.†

Trimethylene chlorobromide and magnesium. Trimethylene chlorobromide usually did not react with magnesium in dry ether without a catalyst. In one instance, after carbonation in the usual manner, the total acid was found to be equivalent to 8% of the halide used; glutaric acid was identified by a mixed melting point determination, and the characteristic disagreeable odor of γ-chlorobutyric acid was very noticeable.

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*This substance was donated by Shawinigan Chemicals Limited.

†*The writers are indebted to Professor Adkins of the University of Wisconsin for carrying out these reductions.*

THE ALKALOIDS OF FUMARIACEOUS PLANTS

VIII. *CORYDALIS AUREA*, WILLD. AND THE CONSTITUTION OF BICUCINE[1]

By R. H. F. Manske[2]

Abstract

The chemical examination of the alkaloids of *Corydalis aurea* has shown an unusual complexity and of the total of more than ten alkaloids thus far isolated only six are now described. The record deals chiefly with the stems and leaves of the plant in which protopine was present in exceptionally low concentration (0.025%). Equally exceptional is its high concentration in the roots (1.6%). *l*-Tetrahydropalmatine constituted the largest fraction of the remaining alkaloids, and its present isolation is the first on record although the *d*-form was previously known. Two new and well-characterized alkaloids, which have been named *capaurine* and *capauridine*, respectively, are isomeric and are best represented by the empirical formula $C_{21}H_{27}O_5N$. Both contain one phenolic hydroxyl and four methoxyl groups, and yield on methylation non-phenolic bases which do not appear to be identical. The presence of two bases, bicuculline and bicucine, which were first recorded in this series of papers, has again been demonstrated.

The constitutional analysis of the new bases, as well as the isolation and characterization of the minor alkaloids, is in progress.

In an appended note it is shown that bicuculline and bicucine are closely related and interconvertible. The latter is the free γ-hydroxy acid of which the former is the lactone.

With the exception of *Corydalis sempervirens*, *C. aurea*, Willd. (*Capnoides aureum* (Wild.) Kuntze) is the only species of this genus which extends its natural habitat to central and eastern Canada. According to several botanists whom the writer has consulted it grows well only on burnt areas or recent clearings, and it was in such habitats that the material for the present investigation was found. It was collected late in 1933, the glaucus blue foliage having partly turned to a dull reddish-yellow. The roots were severed from the aerial parts before drying and examined separately.

Owing to the fact that the contained alkaloid mixture is extremely complex, no fewer than ten apparently pure bases having been thus far isolated with the certain indication of still others, it seemed advisable to place on record some of the information obtained to date. Furthermore, a second lot of plant material is in process of examination and it is hoped that the combined mother liquors from the two will yield not only new bases but sufficient quantities of those present only in traces for adequate characterization.

Heyl (1) reported the presence of protopine and a second base (melting at 148-149° C.) in the roots of *C. aurea*, and this seems to be the only investigation on record concerning the plant. Although the roots have not been adequately investigated no indication of Heyl's second alkaloid has been found in the stems and leaves. Protopine was present in the dried roots to the astonishing amount of 1.6% while its presence in the stems and leaves was limited to no more than 0.025%, this in spite of a total alkaloid content

[1] *Manuscript received September 29, 1933.*
Contribution from the National Research Laboratories, Ottawa, Canada.
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of at least 3.0%. The constituent present in greatest amount in the plant however is *l*-tetrahydropalmatine. The *d*-form of this alkaloid was isolated from *C. tuberosa* and recognized as such by Späth, Mosettig and Tröthandl (5) who suggested its identity with a number of bases obtained by several investigators from various sources. Owing to the present discovery of the *l*-form an element of doubt is raised in some of these cases. Two other bases which were first obtained from *Dicentra cucullaria* (2) but which have since become more familiar, namely, bicuculline and bicucine, were present in tractable amounts.

Only two of the six or seven remaining alkaloids which have been obtained from this plant have been adequately characterized. They are isomeric and analyses are in agreement with the formula $C_{21}H_{27}O_5N$. Both are phenolic (one hydroxyl) and contain four methoxy groups. Inasmuch as they appear to be new the names *capaurine* and *capauridine* are proposed, the first syllables being derived from the generic *Capnoides* Adans. and the remaining syllables from the specific name. Capaurine was obtained to the extent of 0.33% in large, stout pale yellow prisms, appreciably soluble in hot methanol and melting at 164° C.* On methylation with diazomethane a non-phenolic base, $C_{22}H_{29}O_5N$, containing five methoxyl groups was obtained.

Capauridine was obtained to the extent of 0.018% in colorless fine needles practically insoluble in boiling methanol and melting at 204° C. Methylation does not yield the same methyl ether as that furnished by capaurine, though presumably the two are isomeric.

Experimental

Throughout this investigation it was found advantageous to follow strictly the procedure detailed in a communication dealing with *Adlumia fungosa* (4), and in the following record the designations of the various fractions have the same significance. There was available 6.5 kilos of the dried stems and leaves, and except where specified the roots are not included in the following.

Isolation of Protopine

The precipitate (BS) consisted of a dark amorphous mass weighing only 3 gm. An appreciable amount of inorganic matter was removed by filtering a chloroform solution of this through a layer of charcoal. Evaporation of this to a syrup and addition of hot methanol and a nucleus yielded pale yellow crystals of protopine which, when recrystallized as hydrobromide, regenerated and again recrystallized, melted at 211° C., either alone or in admixture with an authentic specimen. An identical treatment of 195 gm. of the roots yield 3.2 gm. of once-recrystallized protopine, which after two further recrystallizations weighed 3.0 gm.

Isolation of l-Tetrahydropalmatine

The solution (SR) on slight cooling yielded a copious crop of pale yellow crystals. This was filtered off, washed with water and with ether (LC) and recrystallized from hot water. More of this salt was obtained from the com-

**All melting points are corrected.*

bined mother liquors (ASR) and a further quantity from the non-phenolic bases (BC). Repeated recrystallization yielded almost colorless needles melting at 232° C. to an orange melt, some sintering taking place at about 220° C.

A small portion of this was dissolved in hot water and cautiously treated with ammonia. The caseous precipitate rapidly crystallized. It was filtered off, washed with water, dried, and recrystallized from hot methanol in which it is moderately soluble. Large, stout, flat prisms with pyramidal terminations were thus obtained. The melting point is sharp at 142° C. In concentrated sulphuric acid it dissolves to a colorless solution which on heating becomes dirty greenish-brown and then turns to a deep brilliant purple which becomes red on dilution with water. Most characteristic is the fact that the crystals are triboluminescent, a livid blue light being emitted when they are rubbed with a glass rod in a dark room. These observations together with the analytical figures are sufficient to identify the base as tetrahydropalmatine. The optical rotation $[[\alpha]_D^{22}, -278°$ (c = 2.00 in 95% ethanol)] characterizes it as the *l*-form. Oxidized with iodine in alcoholic solution it yielded the sparingly soluble palmatine iodide melting at 243° C. Calcd. for $C_{21}H_{22}O_4N$: C, 70.99; H, 7.04; N, 3.94; 4 OMe, 34.93%. Found: C, 70.83; H, 6.82; N, 4.26; OMe, 34.87%.

Since *dl*-tetrahydropalmatine melts at 144° C. an equal mixture of the two forms should melt at a temperature not less than 142° C., the melting point of each form. In accordance with this supposition, a mixture of approximately equal amounts melted not quite sharply at 142–144° C. when slowly heated. The author is greatly indebted to Professor Ernst Späth of the University of Vienna for this specimen of natural *d*-tetrahydropalmatine.

Isolation of Capaurine and Capauridine

The precipitate (BCE) consisted of 27 gm. of an easily filterable granular product. It was suspended in 200 cc. of methanol and the mixture boiled for some time. After thorough cooling the separated crystalline material together with that not originally dissolved was filtered off and washed with cold methanol. This was dissolved in hot chloroform and the filtered solution (charcoal) evaporated to a syrup, and then repeatedly evaporated with fresh portions of methanol until crystallization in the hot liquid began. The colorless crop of fine crystals was filtered off and washed with cold methanol. As thus obtained *capauridine* melts at 203–204° C. some darkening taking place at 180–190° C. Recrystallization from chloroform-methanol did not improve the appearance, nor did it raise the melting point above 204° C. With concentrated nitric acid an intense cherry-red color was immediately developed. Calcd. for $C_{21}H_{27}O_5N$: C, 67.56; H, 7.24; N, 3.67; 4 OMe, 33.24%. Found: C, 67.64; H, 6.77; N, 4.08; OMe, 33.05% (mean of duplicates). This formula is at present preferred to the one with two hydrogen atoms fewer, because such a formula would almost certainly require an aporphine or protoberberine structure with five oxygen substituents, not a single

representative of which is known. On the other hand, the closely related benzyl-tetrahydroisoquinolines offer greater scope for the introduction of O-substituents. The total yield of capauridine was 1.2 gm.

The filtrate from the crystallization of capauridine on cooling and scratching yielded a copious crop of a second alkaloid. When once obtained crystalline this was only sparingly soluble in hot methanol from which it was recrystallized. After two such operations *capaurine* was obtained in very pale yellow, stout, irregular prisms, melting sharply at 164° C. In cold concentrated nitric acid it dissolves with the production of an intense cherry-red color passing into brown on heating. Cold concentrated sulphuric acid dissolves it to a colorless solution which, on heating, suddenly develops a very intense brown color which is changed only in intensity on dilution with water. Calcd. for $C_{21}H_{27}O_5N$: C, 67.56; H, 7.24; N, 3.67; 4 OMe, 33.24%. Found: C, 67.66; H, 6.70; N, 3.98; OMe, 33.15% (mean of duplicates).

The arguments against a formula with two hydrogen atoms fewer are the same as in the case of capauridine, although in both cases such a formula would agree equally well with the analyses.

Some more capaurine as well as a small quantity of capauridine was obtained from the fraction (EC), making the total yield of the former 21.4 gm.

Methylation of Capaurine

One gram of the base was dissolved in hot methanol and the rapidly cooled solution treated with 5 gm. of nitrosomethylurethane. A saturated methanolic solution of potassium hydroxide was cautiously added until an excess was present. The mixture was placed in the ice chest for six hours, then somewhat diluted with water and the methanol distilled on a steam bath. The insoluble pasty base was gathered on a glass rod and washed with water. It was then stirred up with aqueous potassium hydroxide containing a little methanol. The product, which rapidly became granular and crystalline, was filtered off and thoroughly washed with water. After drying it melted at 150-151° C. Recrystallization from hot methanol in which it is only sparingly soluble yielded stout, colorless prisms melting sharply at 152° C. Calcd. for $C_{22}H_{29}O_5N$: C, 68.22; H, 7.49; N, 3.62; 5 OMe, 40.05%. Found: C, 68.20; H, 7.11; N, 4.07; OMe, 40.55%.

Methylation of Capauridine

The procedure described for the methylation of capaurine was closely followed, except that owing to its sparing solubility the suspension of the fine crystals in methanol was employed. The quantities used were 0.3 gm. of the base and 2 gm. of the nitrosourethane. As before the crude base readily crystallized. It was recrystallized twice from hot methanol in which it is readily soluble. As thus obtained it consisted of colorless, stout needles melting sharply at 142° C. When admixed with an equal quantity of capaurine O-methyl ether the mixture began to sinter at 135° C. and melted completely at 140° C. The substance has not yet been analyzed.

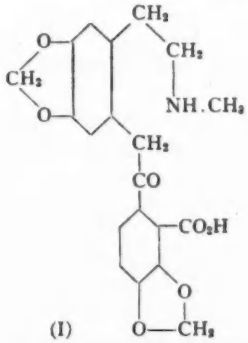
Isolation of Bicuculline and Bicucine

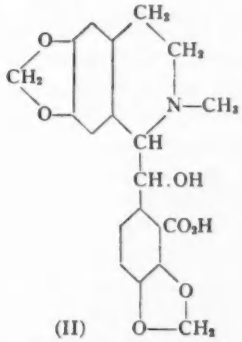
The mother liquors from the isolation of the *l*-tetrahydropalmatine were extremely complex and this complexity was not greatly lessened in the fractions (EC) and (BCE). The combined mother liquors from which no more capaurine and capauridine could be obtained were exactly neutralized with concentrated hydrobromic acid, largely freed of solvent and repeatedly evaporated with chloroform. The thoroughly anhydrous solution deposited a small amount of gummy material which was removed by filtration through a layer of charcoal. The somewhat concentrated filtrate was treated with ethyl acetate until the incipient turbidity just disappeared on shaking and gentle warming. During the course of several days a colorless hydrobromide separated. This was cautiously washed with a mixture of methanol and ethyl acetate and the base regenerated by treating a warm aqueous solution with ammonia. The base which rapidly became granular was filtered off, washed, dried and recrystallized from chloroform-methanol. There was thus obtained 3.9 gm. of stout, colorless prisms, melting sharply at 177° C. The resolidified substance melted at 194-195° C. and this dual behavior was repeated when a specimen of bicuculline from *D. cucullaria* was admixed with it.

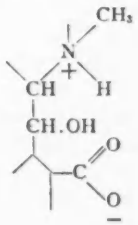
The mother liquor from the above-mentioned bicuculline hydrobromide was freed of organic solvents, dissolved in water, and the clarified solution fractionally precipitated with ammonia, the liberated bases being thoroughly extracted with ether at each stage. Of the five fractions, the first consisted almost exclusively of bicuculline, while the second and third yielded a little more (total 0.2 gm.). The remaining fractions could not be induced to crystallize. They were therefore combined, dissolved in dilute hydrochloric acid and basified with excess potassium hydroxide. The alkaline filtrate on saturation with carbon dioxide yielded a semicrystalline base which was filtered off, washed with water and dried. Extraction with chloroform and with cold methanol left 0.2 gm. of almost colorless crystals which melted at 209° C. This base was dissolved in cold concentrated ammonia solution and the clarified filtrate allowed to remain in a partial vacuum over concentrated sulphuric acid. In the course of 24 hr., fine colorless needles of *bicucine* melting either alone or admixed with an authentic specimen at 217° C. had separated.

The Constitution of Bicucine

During the course of a further investigation of *D. cucullaria*, having as its object the isolation and characterization of the minor alkaloids, a considerable quantity of bicucine has become available and it has gradually become evident that it bears an exceptionally close relation to bicuculline. In the first place the two alkaloids have been invariably found together in the same plant and the possibility of their interconversion seemed a reasonable one. It has now been shown that hydrolysis with excess alkali is sufficient to convert bicuculline into bicucine, the latter being precipitated from the alkaline solution by a stream of carbon dioxide. Two formulas (I) and (II) are therefore possible.


(I)


(II)


(III)

The first was preferred for some time because it bears the same relation to bicuculline that nor-narceine bears to narcotine, although this change is brought about by a different method. Furthermore, a substance of formula (II) would be expected to form an anhydride with exceptional ease and yield the alkaloid bicuculline. It had been previously observed that oxidation with alkaline permangate yields 3 : 4-methylene-dioxyphthalic acid, but direct evidence for the existence of the 4 : 5-methylene-dioxy grouping was not then available.

The reconversion of a substance of formula (I) into bicuculline is however quite inconceivable and the fact that, as now observed, boiling with dilute hydrochloric acid brings about an equilibrium transformation, definitely favors formula (II) in spite of its stability under other conditions. Furthermore, a solution of the base in either acid or alkali is optically active and formula (I) cannot accommodate this fact.

The stability of the γ-hydroxy acid complex is probably due to the fact that the alkaloid represents a comparatively stable dipole as shown in formula (III). The function of a strong acid in causing the formation of the lactone is therefore not only that of a catalyst in esterification, but more especially the removal of the charge from the carboxyl and the restoration of its normal properties.

The bicucine used in the following experiments was purified by solution in concentrated ammonia solution and removal of the ammonia from the filtered solution in a desiccator over sulphuric acid. The crystalline product was washed with cold water, dried and washed with chloroform. As thus obtained it melted at 215° to 217° C., but a specimen recrystallized twice from hot water and dried for 48 hr. at 60° C. melted with only slight decomposition at 222° C. This is the monohydrate, $C_{20}H_{19}O_7N.H_2O$. In $N/1$ hydrochloric acid it showed $[\alpha]_D^{25}$, $-145°$ ($c = 0.80$) 30 min. after solution and $-100°$ 24 hr. later, and in $N/10$ potassium hydroxide it showed $[\alpha]_D^{25}$, $-115.4°$ ($c = 3.20$). Obviously the mutarotation is due to the slow conversion of the base into bicuculline. Owing to the slight color in these solutions the above values are to be regarded as approximations only.

Conversion of Bicucine into Bicuculline

Forty-four grams of bicucine was dissolved in boiling dilute hydrochloric acid and the solution heated on a steam bath for several hours. The solution was cooled somewhat and cautiously treated with aqueous potassium hydroxide until the mixture was distinctly alkaline to litmus. The precipitate was removed with a glass rod and thoroughly washed with boiling water. After drying it was dissolved in chloroform, the solution clarified with charcoal and the filtrate freed of solvent. The thick residual syrupy liquid was treated with hot methanol. Seeding with a crystal of bicuculline induced immediate crystallization. The yield of pure base melting at 177° C. (the resolidified base melting at 194-195° C.) was 15 gm.

The alkaline solution from which the bicuculline had been precipitated was made almost neutral with hydrochloric acid. The addition of aqueous sodium bicarbonate caused the rapid crystallization of bicucine: recovery, 11 gm. The process was repeated with some of the recovered base and yielded another lot of bicuculline. The optical rotation of a specimen of carefully purified bicuculline from *D. cucullaria* was determined in chloroform and showed $[\alpha]_D^{25}$, + 130.5° (c = 4). Hydrastine in the same solvent is levorotatory (−67.8°) and it is not improbable that the two bases possess a different orientation of the asymmetric centres. In this connection, Prof. V. E. Henderson of Toronto University, in whose laboratory the pharmacology of bicuculline is being investigated, has found that it is 50–100 times as toxic as hydrastine. Since the physiological action is largely associated with the isoquinoline nucleus, the benzyl-lactone group serving largely as a modifier, slight changes in the latter would scarcely be expected to bring about such an increase in toxicity. Having in mind however the frequent inequality as to physiological activity of optical enantiomorphs, an explanation of the unusual toxicity of bicuculline is possible.

Oxidation of Bicucine with Permanganate

A solution of bicucine in a large volume of dilute potassium hydroxide cooled with ice was treated with a saturated solution of potassium permanganate until the color was permanent for 15 min. The precipitated manganese dioxide was filtered off and the filtrate acidified and repeatedly extracted with ether. The residue from the extract was evaporated twice with alcoholic ethylamine and the solid distilled under greatly reduced pressure. The solid distillate after one recrystallization from ethanol yielded colorless fine needles of *N*-ethyl-3 : 4-methylenedioxy-phthalimide melting at 130° C. either alone or when admixed with a specimen prepared from bicuculline (3).

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STUDIES ON THE APOIDEA OF WESTERN NOVA SCOTIA WITH SPECIAL REFERENCE TO VISITORS TO APPLE BLOOM[1]

By C. E. Atwood[2]

Abstract

This paper describes the results of studies on the wild bees of Nova Scotia, which were carried out in connection with apple pollination investigations in the Annapolis-Cornwallis Valley, Nova Scotia.

The biology of the Apoidea in general is reviewed from the literature, and a list of bees taken on apple bloom is given. As the members of the genera *Halictus* and *Andrena* were found to be the most important native pollinators, the greater part of the paper is devoted to accounts of the habits and life histories of representative species.

The members of the genus *Andrena* were found to have a simple type, such as is generally found among solitary bees. The females provision the nest and then die; the larvae develop to the pupal stage in their underground cells, then emerge as adults the following season. All Nova Scotian species studied were one-generation forms.

The bees of the genus *Halictus* show a primitive social organization, more complex in some species than in others. The first brood consists of females only, which are apparently sterile and work at nest construction, the gathering of pollen, etc. They are followed later in the season by a brood of males and females; these females, after being fertilized, hibernate for the winter, while the males die in the fall. The hibernating habits of different species are described, and notes are given on some parasites and inquilines of the two genera.

Introduction

The study of the wild bees of western Nova Scotia was undertaken in connection with an investigation of the pollination of the apple in this region. This project was sponsored by the Federal Department of Agriculture and was under the direction of Dr. W. H. Brittain. During the first two years statistical studies of the numbers present on bloom were made, and these showed the need of more detailed knowledge of the biology of the species concerned. It was immediately apparent that the bees of the genera *Halictus* and *Andrena* were the most important agents concerned except where hive bees were present, and therefore the greatest amount of attention has been given to these groups. In some cases bumble bees appeared to be of considerable importance, but their average number is too small for them to be considered a very large factor. Moreover their classification and life history are well known. Life history studies under field conditions were accordingly made with the genera *Halictus* and *Andrena*, especial attention being given to those species found to visit apple bloom. A classification of the groups has also been attempted.

General Biology of the Apoidea

This group is the largest one among the Hymenoptera aculeata, having been estimated by Friese (4) to contain 20,000 species, the great majority occurring in the warmer parts of the north and south temperate zones. There is some difference of opinion as to the type from which they have evolved.

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Muller (6, 7), von Alten (1) and Friese (4) maintain that bees have evolved from the Fossores, probably by separate evolution from two or more distinct stocks. Roubaud (8), and Wheeler (9), who reviews the conclusions of previous writers on the subject, believe that the Sphecidae and Apidae (Apoidea) have both evolved from some earlier common Bethyloid stock, and that probably the vegetarian habits of bees may be a continuation of the plant-feeding habits of the Phytophaga or saw flies and their allies.

The great majority of bees are solitary, *i.e.*, one female makes a nest, provisions it, lays her eggs, and dies before the young emerge as adults. Their habits as a whole are "very monotonous," as Wheeler says, although there are individual differences for every species. The nests are made in wood or in the ground, or in crevices in stone. Many use the deserted holes of other bees, or of wasps, beetles and earthworms; Fabre and later writers mention several species which make use of empty snail-shells. Others construct cells from bits of leaf, clay, resin, down from plants, films of salivary secretion and other materials. Inside the cells a mass of pollen moistened with nectar is placed; this may be in the form of a smooth ball, or may be of a more or less fluid consistency and conform to the shape of the bottom of the cell. In this pollen an egg is laid; the entrance to the cell is then closed and the egg hatches and develops to the pupal stage in the cell. Many solitary bees build their homes in groups, and a few even use a common entrance, but there is apparently no approach to the social condition, except in the groups mentioned below. Typical genera of solitary bees are *Andrena*, *Melissodes*, *Ceratina*, *Megachile* and *Osmia*.

The typically social bees belong to the genera *Allodape* and *Halictus*, and to the subfamilies Bombinae, Meliponinae and Apinae of the Apidae. Only certain species of the first two groups are social, while all the species of the last three are. Wheeler (9) considers that the social habit has arisen separately in each of these groups, and that *Allodape*, although its social life is very primitive, is not in any sense ancestral to the higher forms. Brauns (2) has described the habits of this genus and states that they usually nest in pithy stems, as *Ceratina* does, but may occasionally be found in the ground. The female makes a nest or clears out an old one, then lays an egg. When this hatches she brings pollen to feed the larva, thus differing from the solitary bees which first provide the food, then lay the egg. When the first females emerge they help for a time to feed the young brood but eventually form colonies of their own. In the more primitive species, a large mass of pollen is brought to the larva at one time which suffices to feed it until it pupates, but in other species the provisioning is progressive, each load of pollen being divided among several larvae. In the former case also the eggs are very large and are laid at fairly long intervals, while in the latter they are small and several are laid almost at the same time.

There has been a great deal of controversy about the nesting habits of *Halictus*, and in fact various groups within the genus have decidedly different habits. The different types will be discussed under the treatment of that

genus but may be briefly indicated here. The nest is usually in the ground but may be in rotten wood, and is started in spring by one or more overwintered fertilized females and consists primarily of a narrow tunnel with cells excavated along it. These cells may be single, in groups, or, in two European species at least, in the form of a rude comb. The female kneads a mass of pollen moistened with nectar into a nearly round pellet and lays a single egg upon it. The grub hatches, devours the pollen, pupates and finally emerges by digging through the earthen plug which the mother places in the mouth of its cell. Some species of *Halictus* have only one generation; others have two, both containing males and females. Both these types are truly solitary. In yet another species the first eggs develop into sterile females which correspond to the workers of *Bremus*. These help the mother in the provisioning of the nest. She stays in the tunnel, guards the entrance and lays more eggs of which those laid last in the season produce some males and some females. The males die after fertilizing the young fall brood of females; the latter hibernate, and in the spring form a new nest or clean out the old one to receive their progeny. The mother dies at the end of the season along with the males.

The *Bremus* colony is usually started each spring by a single fertile queen, much as in some types of *Halictus*. The queen produces sterile female workers through the summer; males and females toward fall; the females hibernate after mating, while the males die. In some tropical species colonies are said to be perennial and new colonies are formed by swarming instead of by the dispersion of the fertile females in the fall, but in all species in the temperate zones the old queens die each fall.

The *Melipona* colony consists of a fertile female and several sterile female workers, her sisters, which have "swarmed" from the parent colony. The *Apis* colony also consists of a fertile queen and a number of sterile females or workers, but in this case it is the mother which heads the swarm from the old colony, taking with her some of her daughters and leaving the colony to a fertile daughter queen and a number of sterile daughter workers. Males are produced only at certain periods in both these types.

List of Bees Taken on Apple Bloom

Ceratina calcarata Robt. (1 specimen)
Megachile sp. (1 specimen)
Nomada sp. (1 specimen)
Sphecodes sp. (1 specimen)
Osmia spp. (1 female, 3 males)
Bremus ternarius Say.
B. terricola Kirby
B. vagans Smith
B. fervidus Fab.
B. borealis Kirby
B. perplexus Cres. (?)
Psithyrus sp.
Halictus viridatus Robt.
H. foxii Robt.
H. macoupinensis Robt.
H. pectoralis Smith
H. arcuatus Robt.
H. provancheri D.T.
H. rubicundus (Christ.) Kby.
H. coriaceus Smith
H. pilosus Smith
H. cressonii Robt.
H. zonulus Sm.
H. leucozonius (Schrank.)
Andrena milwaukeensis Graen.
A. wilkella Kirby
A. bradleyi Vier.
A. thaspii Graen.
A. vicina Smith
A. carlini Ckll.
A. crataegi Robt.
A. miranda Sm. (*A. hippotes* Robt.) (?)
A. rugosa Robt.
A. mariae var. *concolor* Robt. (?)
A. lata Vier.
A. grandior Ckll.
A. ceanothi Vier.

Relative Abundance of Species

Exact data on the relative abundance of the various species of wild bees which visit apple are rather hard to obtain. The characters which separate many of the species are microscopic, so that an observer can determine the bees seen on the flowers only in a very rough way by deciding that they belong to one of two or three general groups. For example, it would be scarcely possible to separate *H. viridatus* Lov., *H. foxii* Robt., *H. cressonii* Robt., and possibly one or two other similar species, without a closer inspection than is usually obtained in the field. Even a count of species collected from bloom does not give a very definite idea of the numbers present, because of the fact that some are very easily captured while others are readily alarmed and difficult to net. However, from the combined results of four seasons' collecting and observation, a general idea has been gained of the numbers present belonging to the various groups.

It is quite apparent from even a short superficial observation that the small *Halicti* of the *viridatus* group mentioned above are more numerous than any other wild bees, provided the weather is suitable for general bee activity. Because of their small size (mostly less than 8 mm.) and rapid flight they usually pass unnoticed by the fruit growers, who do not realize the large part played by them in pollination throughout the orchards of the valley.

Probably second to these in numbers are some of the members of the genus *Andrena*. There is considerable local variation in the numbers of the different species present. In some areas *A. crataegi* Robt. is the most numerous; in others *A. wilkella* Kirby. *A. carlini* Ckll. and *A. vicina* Smith are often present in fair numbers, and from their large size and industrious habits are probably of great value. It is nearly always the female of these last two species which is taken on apple, whereas a large proportion of *crataegi* and *wilkella* are males. At one station *A. thaspii* Graen. was taken in considerable numbers, but as a rule this species appears to emerge too late to be of much value. Another group of *Halicti* which supplies a fair number of workers in orchards is composed of *H. rubicundus* (Christ.) Kby., *H. leucozonius* (Schrank.), *H. zonulus* Smith, and *H. coriaceus* Smith, while *H. arcuatus* Robt. is numerous in some localities. A bee which has been identified as *A. rugosa* Robt., and several closely allied species were present in the orchard at the Experimental Station, Kentville, in 1932, but were not found to be numerous at any of the other places where collecting was done. The other *Halicti* and *Andrenae* listed above may be regarded as occasional visitors only.

When present in appreciable numbers, the bumble bees of the genus *Bremus* undoubtedly are of considerable value, but the counts taken on apple bloom show that they are far outnumbered by the other wild bees. The numbers of bumble bees represented in the counts may not indicate their true value, because of the fact that they seem to prefer the tops of the trees, while most of the counts were taken within 10 ft. of the ground. Also they work at lower temperatures and in cloudy weather when other wild bees are not present. In an orchard at Blomidon during one season these insects were numerous

enough to be an important factor in pollination, but this is an exception to the general rule. The most numerous species seen in Nova Scotia orchards is *B. ternarius* Say, followed by *B. fervidus* Fab. and *B. vagans* Smith. Other species of *Bremus* and *Psithyrus* are occasional visitors only. The other bees given in the list must be regarded as largely accidental. Both *Osmia* and *Nomada* are present during apple bloom, but prefer blueberry, rhododendron, and other wild bloom.

Flies of many species, ranging in size from very small midges up to the large Syrphus flies, are frequent visitors at apple bloom. According to the counts taken of visitors to the blossoms they are much more numerous than bumblebees, but less numerous than other wild bees. However, it is very doubtful if the frequency of their visits can be taken as an index of their usefulness. Many of the flies recorded from apple do not come in contact with the stigmas at all because they simply alight on the petals and eat a small quantity of pollen, without entering the flower as the bee does. The flies, of course, have no interest in gathering pollen, they are simply eating a small quantity to satisfy immediate needs. Others, however, especially the Syrphidae and Bombyliidae alight on flowers and walk over the stamens and pistils much as the bees do. Although pollen-collecting apparatus, such as bees have, is absent, a fair number of loose grains adhere to the body hairs, and are transported from flower to flower. The counts on bloom show also that the number of flies present fluctuates in a very erratic manner, and it is apparent that they cannot be relied upon to effect adequate pollination in the absence of other agents.

Notes on the Life Histories of Bees Taken on Apple Bloom

The following life history notes on some representative species of bees taken on apple bloom are compiled from observations made during the seasons 1929-1932. The method of study consisted of observations on the bees at work in the field, and statistical analyses of nest contents. In most cases individual nests were excavated and their contents noted, but in others the tunnels were so close together in the ground that it was impossible to follow single holes to their end or to ascertain their contents accurately. Therefore in some of the counts only the totals for an area excavated are given. The most extensive observations were on the genus *Halictus* as they persist throughout the summer, whereas each species of *Andrena* lasts for a few weeks only; moreover their nesting habits are comparatively simple and are much better known than those of the *Halicti*.

In 1931 some attempts were made to rear the *Halicti* in artificially constructed cells. None of the attempts were successful in rearing the insect from egg to adult, although larvae which had pupated emerged successfully. The chief difficulty was in controlling moisture conditions; the larvae were readily attacked by a mold when removed from the cells in which the egg had been laid, if kept moist; on the other hand the larvae rapidly succumbed to any condition approaching dryness.

None of the bees whose life history has been studied appear to confine themselves to any one family of plants in gathering pollen. Most of those found on apple may be taken at the same time on *Vaccinium*, *Rhododendron*, *Amelanchier*, *Prunus*, *Fragaria*, *Taraxacum*, etc., as well as on other plants which are in flower after the apple bloom has gone.

1. *Halictus arcuatus* Robt.

The nests of this bee were found in one place only. In this area, which occupied the upper slope of a steep pasture, there was a community consisting of hundreds of holes. The slope was composed of a loam with the following components:—sand, 69.4; silt, 21.8; clay, 7.8; volatile matter, 2.6-3.4%; and numerous small boulders. It was sparsely covered with grasses and weeds such as asters, goldenrod, thistles, wild carrot, and similar plants of hillside pastures. Nests were made either in the small areas of bare soil or among the roots of the grasses and weeds.

The entrances to the nests were usually very inconspicuous and difficult to discover. They were roughly oval in outline, but irregular, resembling the weathered burrow of an earthworm. Inside the entrance the tunnels were circular in cross section, very crooked, and more nearly on the horizontal plane than those of any other species studied. The cells in which the pollen was stored and the young reared were ovoid, joined to the main tunnel by a narrow neck, and finished inside with a smooth waterproof coating made of fine clay mixed with saliva. The pellets were larger in proportion to the size of the bee than those of the other species studied, and somewhat flattened instead of being spherical.

H. arcuatus begins its activities early in the spring. It is a common visitor to apple, wild cherry, etc., and, as early as May 18, holes were found containing fully formed pellets. Since the females do not hibernate in the summer holes, the nests found at this time must have been completely excavated since the bees began work. Therefore it probably emerges from hibernation in April or early May.

The eggs are white, translucent, narrowly elliptical, and slightly curved, so that they fit closely to the surface of the pollen pellet. When it hatches the larva feeds on the pollen pellet until it has consumed it, then pupates and finally emerges as an adult. Owing to the underground habit of the bee and the difficulty of rearing artificially, the exact length of the various stages could not be definitely ascertained. However, some notes made on the time at which different stages were found give a general picture of the life history.

The first larvae appear about the first week in June; the first pupae about June 20. The pupae seen at this time are all females and may be distinguished by their large size and stoutness. These females remain in the nest and bring in more pollen to provision cells. Whether or not they lay eggs has not been determined. An occasional male pupa may be found as early as July 15, but as a rule the greatest numbers begin to appear about two weeks later. Slightly later than this again the fall brood of females appears and by the end of August practically all pupae have emerged. About this time all the females

except the fall brood apparently die, while the latter, after mating, seek some other locality for hibernation. Males and females were never observed *in copula*—but mating probably takes place on flowers. The hibernating place of this species has not been discovered, but it is not on the site of the summer colony as careful digging there in the fall failed to show any signs of hibernating bees. From the fact that two females have been taken in one tunnel in the spring before larvae could possibly have developed, it would appear that two bees sometimes co-operate in digging the summer nest when they emerge in spring, and several may hibernate in the same hole.

Very few parasites were found in the holes of this species. In 1930 several newly hatched *Sphecodes* were found in one hole which was excavated, but none were taken from nests in 1931. A Conopid fly was very numerous in this region and dozens of them could usually be found nesting on grass leaves. They were often observed to dash at bees as they flew past and strike them in mid air, whereupon both would fall to the ground and struggle for a few seconds. The bees seemed much alarmed by these attacks, and as the Conopidae are known to lay eggs on other adult insects in this manner it was thought that the flies were probably parasitizing the bees (*vide* de Meijere, (5)). However, the great majority of the flies seen on the grass were males, and upon further observation they were observed to strike females in mid air in precisely the same way as those seen pursuing the bees. None of those seen attacking or striking bees were females, so the question is not definitely settled. It may be possible that the males mistake passing bees for female flies. The flies were, however, never observed to enter the nests, and no maggots were found.

Owing to the nature of the entrance, it was impossible to measure the number of holes in a given area, but instead an analysis of a given area was made in 1931 and 1932. In 1931 an area of 9 sq. ft. gave 109 pellets, 4 pupae, and 78 adults or 191 insects in all stages. Similar excavations in 1932 indicated a population of 198 per sq. yard. In the latter count many dead adults were found in the soil, probably the result of much wet cold weather in the spring.

This species apparently has two forms of female, the spring form being larger and more robust, with more pronounced abdominal fasciae and a shorter dorsal space to the propodeum. The smaller form has been taken frequently on flowers during the summer and was also found living in nests with the larger females. The question is considered more fully in the paper on the taxonomy of this genus.

2. *Halictus leucozonius* Schrank.

This member of the genus nests in a great variety of situations and is very plentiful and very widely distributed in the Annapolis Valley region. The favorite habitat appears to be a somewhat flat field or pasture covered with short thin grass, the character of the soil apparently not being an important factor, as long as it is firm and not composed of coarse gravel or pure sand. Many large communities were found in pastures of this character, but nests

were also commonly found along roads and ditches, between rows of trees in orchards, on open clay or loam banks and the drier parts of open diked lands.

The entrance to the nest of this species is $\frac{1}{6}$ to $\frac{1}{4}$ in. in diameter at the entrance, slightly wider inside, and usually enters the ground perpendicularly. As a rule it is straight for the first two or three inches, and sometimes for the whole length, although there is usually a slight crook somewhere in the tunnel. Around the entrance there is always a low mound of earth, except on a slope where the earth falls downward as it is brought out. This mound is about $1\frac{1}{2}$ in. or more in diameter, and is hollowed at the top so as to form a crater about the entrance. The tunnel and cells are lined with the usual waterproof lining. The latter are about $\frac{1}{2}$ in. long, ovoid in shape, and joined to the main tunnel by a neck slightly longer than the length of the cell. This neck is generally filled with earth after the cell has been provisioned.

The females of this species do not begin nest building much before June 1. In some cases two females must co-operate in digging, because more than one adult was occasionally seen in a hole much earlier than the appearance of the pupae in the cells. There are also great differences between the times of nest building of the females. For instance, in one location with a heavy clay soil, many newly made nests were found on July 21, while, a few feet away, other holes of the same species contained larvae and pupae.

During the provisioning of the cells the adults have a curious habit of digging out some earth from down in the tunnel, probably from the cells, pushing it up as far as the mouth of the hole and leaving it there where it forms a plug slightly below the level of the top of the cone around the entrance. This plugging of the nests was found to take place in many nests between 11 a.m. and noon. The plug was sometimes removed in the afternoon, sometimes left until next morning. The females do not usually stand guard at the mouth of the tunnel, so this plug may act as a sort of door to keep out intruders. It must be quite effective, because very few parasitized cells have been found while excavating holes of this species.

It would appear from the counts of larvae, pupae, and adults from excavated holes that there is no great emergence of females before the appearance of the males, because males were found within a few days of the discovery of the first pupae. This would indicate that the only females produced are those which hibernate during the winter, although this is not definitely proved.

The habits of the males of this species are similar to those of *H. rubicundus* (Christ.) and *H. provancheri* D.T.; that is, they wait in holes and crevices and around sunny open spots for the appearance of females. They also are taken on goldenrod, fall dandelion, and other flowers in large numbers, but mating probably takes place in the former situations, although it has not been observed.

Apparently the females do not hibernate in the summer nesting site, as such areas have been searched without finding any dormant bees. The males persist until late in the fall; some were noted on October 10 after rather severe frosts.

Attempts were made to estimate the numbers present in some of the more densely populated areas. Counts taken on measured areas in 1931 gave an average of six to seven holes, or between 25 and 30 bees per square foot. This would perhaps be a rather large estimate for a pasture or field with a small population, but there were large areas near Grand Pré, Horton, Welsford, Port Williams, and other locations where this figure would not be excessive.

H. zonulus Sm., a closely related but rarer species in Nova Scotia, has very similar habits, to judge from the few nests found. It apparently prefers somewhat flatter and more moist locations for its nest.

3. *Halictus rubicundus* (Christ.) Kby.

This species is the largest one of the genus found in Nova Scotia, and is frequently seen on apple bloom. It nests in various types of soil, the holes usually being very scattered, but in one location an extensive colony was found nesting on the inner face of a dyke. This dyke was composed of sods cut from the silt brought down by the river, and held together by the roots of sedges and grasses. In other localities the holes were chiefly found in rather dry firm soil, sparsely covered with grasses.

The hole is usually $\frac{1}{4}$ in. or more in diameter at the mouth, slightly larger inside, nearly perpendicular to the surface, and usually straight or at most with a slight turn about halfway down, although some are more crooked. The holes seldom reach a depth of more than 8 in. They are usually simple, but occasionally a branched one was found, which had apparently been made by two females using a common entrance. Around the top of the nest a small cone of loose earth is usually found, unless the hole is situated on a slope.

The cells are of the usual type, oval, $\frac{1}{2}$ in. or more long, with a smooth firm lining, and joined to the tunnel by a narrow neck.

H. rubicundus begins work sometime in early May, at least in the lighter soils, as completed cells were found as early as May 20. The first summer females emerge as a rule about the middle of July or a little earlier, the males appearing some two weeks or more later. Other females and males continue to emerge until well on in August. The males wait in holes and on open sunny spots for the females to appear and mating takes place on the ground; they are also, however, found on various flowers drinking nectar.

The fertilized females may dig new holes in which to hibernate, or may merely dig a summer nest a few inches deeper, and partly fill the upper section with loose earth. Hibernation appears to take place at a depth of about 12 in. below the surface. It begins about August 20, and by September 1 most of the females have disappeared, although the males remain until killed by frosts.

A few cells were found which contained the maggots of a parasitic fly, but no other enemies of the bee have been discovered in this region.

4. *Halictus provancheri* D. T.

No nests of this bee had been seen before the spring of 1931, although the holes made by two hibernating females had been found the previous summer. The preferred habitat of the species seems to be a well-drained soil with a covering of short grass or other low vegetation. In each nesting site found, except one, the soil was light and rather loose; the exception being the dyke described as a nesting site of *H. rubicundus*, which had been made from sods of a brackish marsh. A covering of short grass or other vegetation appeared to be an essential feature of the nesting site, as every hole found was in such a situation.

The nests of this bee were more difficult to find than those of any other *Halictus* studied. The entrances were always practically invisible until a bee was seen to enter one, and even then the debris on the surface usually fell together over the hole as soon as the bee had entered. Most tunnels opened either at the base of some plant or else actually among the stems of a grass clump. Owing to the light dry nature of the soil in which the nests were made it was impossible to excavate them in such a way as to observe the structure very carefully, but they were apparently nearly vertical after the first inch or so, the upper part coming in at an acute angle to the surface and then turning several times before becoming vertical. The cells were of the general *Halictus* type, but not as numerous as those made by other species; five was the greatest number of inhabitants taken from a single hole.

The females had a most annoying habit of hovering around and lighting on grass for an hour or more before entering the hole, even when carrying a load of pollen. In one case, some of these females were watched continuously from 1 p.m. until 4.30 p.m. and had not entered the hole at that time. This hesitation to enter the hole was repeatedly observed, but is rather hard to understand, because it must lead to a great waste of time in pollen gathering. A large number of a species of parasitic fly were observed in and around the nests of this species and they may have had a disturbing influence on the activities of the bee. Many cells were found which contained dipterous larvae, while puparia were often found in the soil near the tunnel, the maggots apparently leaving the cell to pupate. This heavy infestation of parasites may be responsible in part for the comparative rarity of *H. provancheri* in this part of Nova Scotia.

The earliest date on which holes of this species were excavated was June 8. At this time the hole was still in the course of construction but some pollen had been brought in. Young larvae were found some two weeks after this date. Males began to appear early in July, but were most abundant during August, when they were very numerous around the dyke mentioned above. It would appear that very few if any females could emerge before the males begin to appear, so the species must be like *H. leucozonius* (Schrank.), having but one brood per season. The collecting of pollen, however, must be kept up over a considerable period as pupae were found as late as July 31.

Males were taken on various flowers, but were most numerous around open sunny spots near nesting sites, and mating was observed to take place in such localities. It was also, however, observed on flowers in 1932. The females begin to hibernate soon after the middle of August. They dig new holes for the purpose, in light sandy loam, partly filling the hole with loose earth.

5. *H. viridatus* Lov.

This bee is more numerous and more widely distributed than any other species of *Halictus* taken in the apple growing districts, and in spite of its small size it is of great value in orchards, especially as it is about the first of the genus to appear in the spring. Its life history is more complicated and interesting than that of any other species studied, and shows a near approach to the social habit.

Bees of this group have been found nesting in so many types of soil that it is very difficult to state what is, or is not, a favorable habitat. Apparently any firm well-drained soil except pure sand or coarse gravel can be used. A slope is sometimes preferred, but is not at all essential in a nesting site; in some places the uncultivated strip between rows of orchard trees was a favored spot. A bare soil or one sparsely covered with grass is preferred; a few holes were found in thick grass but they were the exception. The soil from two favored sites was analyzed and proved to have the composition shown in Table I.

TABLE I

COMPOSITION OF SOIL

Constituent	Site No. 1	Site No. 2
Sand, %	80.0	79.3
Silt, %	14.8	16.3
Clay, %	4.4	3.7
Volatile matter, %	2.6-3.4	2.6-3.4

South, southeast or southwest slopes were preferred, but nests were found on slopes of all directions, including north. In very favored localities the nests were often so close together as to suggest that the bees were somewhat colonial or rather gregarious in habit, but under average conditions the nests were quite isolated, so the grouping of holes was probably due to the attraction of the favorable site rather than to any preference for the company of other members of the species.

The openings of the tunnels are very regular and smooth, and circular in outline; as a rule they enter the ground nearly at right angles to the surface. Usually no particles of soil were left around the hole, but in some cases, especially where the holes were constructed among grass stems, small cones remained about the excavation, composed of the material removed from the tunnel and cells. Many of the holes were found on smooth surfaces, with no attempt at concealment, but occasionally they were under small leaves or grass blades slightly raised from the ground, or in the angles around projecting lumps of soil, small rocks, etc. In one case a hole was found in an area which was completely covered by a leaf of a young *Hieracium* plant;

the bee had cut a perfectly circular hole through the leaf directly over the entrance of the tunnel. Inside the entrance the tunnels of this group were by far the most complicated of those of any of the bees studied. The mouth is made of a size to fit the head of the bee so that when a female stands just inside the entrance the hole is effectually blocked. Immediately inside this entrance the hole is enlarged to two or three times the diameter of the mouth forming a chamber in which two bees may pass. The chamber is about the shape of an egg glass, with the entrance at a point corresponding to the bottom of the bowl. It narrows abruptly at its inner part to form a constricted passage of the same shape and size as the outer entrance. Beyond this is a second enlarged chamber; a third and fourth each with its round narrow mouth may be present. Inside the last chamber the main tunnel is slightly larger than the entrance, still smooth and circular in section, and lined with the fine clay and saliva mixture which most *Halicti* use.

The majority of holes examined consisted of a single winding tunnel 4 to 8 in., or more, in total length but seldom reaching a vertical depth of more than 6 in., below the surface. They were usually very crooked, winding up, down, or sideways but usually with a straight portion about 3 in. long immediately inside the area taken up by the entrance chambers; this was generally followed by a sharp curve, then various windings were found in the region occupied by the cells. However, not all tunnels were of this simple type, as branched ones were quite frequently observed. The branching in many cases took place just inside the entrance; sometimes it even opened off the first or second chamber. In other holes it took place below the straight portion mentioned above. In the first type, where the tunnel branched near the entrance, each branch often had secondary ones near the bottom, so that they were like two distinct branching tunnels with a common entrance. In some cases it appeared that there was a connection between two such branches near the bottom as well as at the entrance, but the cells of branched tunnels were always placed so closely together that it was hard to discover their exact relations to the main tunnel.

The holes of this group are very populous. It was quite common to find 15, 20, or more, inhabitants in a single tunnel. Only rarely were more than a dozen found in the tunnels of any other species. This may be partly due to the fact that many holes, even in spring, contain more than one female. Apparently when they come out of hibernation, a few of the sisters may scatter and find new homes, but, in many cases, two or more remain in the tunnel in which they passed the winter, dig it out again, reline the cells and work together in storing pollen and rearing young. A very good example of a hole of this kind was seen at Blomidon on June 5, 1931. A bee carrying pollen was seen to alight near a hole which was filled by the head of another female. The guard withdrew into the hole and the pollen-covered bee entered. The hole was then excavated and was found to have two branches which separated just inside the entrance, and to contain four adults, nine pellets with eggs, and two young larvae. It was so early in the season that all these

adults must have been overwintered females; it would have been interesting to have marked them to see if they took turns at standing guard. In any case their behavior is quite different from the species described by Fabre, which do not guard their burrows in the spring but only after the first pupae have emerged as adults.

In spite of the vigilant guard kept by the *Halicti* at the mouth of the tunnel, enemies enter, and many cells inhabited by inquilines were found while excavating the nests of these bees. The most common were the maggots of one of the Diptera, which has not been secured in the adult stage. Many Meloid beetle larvae in the triungulin stage, and one scarabaciform larva, were found. Occasionally an adult *Sphecodes* was found in a nest, but it may be mentioned here that on one occasion a *Sphecodes* was seen vigorously excavating a hole of its own, so it would appear that these females are not always socially parasitic. The guard at the entrance could not keep out the small beetle larvae which enter by clinging to the bee as she enters the nest, but the flies and the inquiline bees must enter when no sentinel is present. Parasitic Strepsiptera were also found more frequently on bees of this group than on any other species of *Halictus*, and many were infested with ticks as well. In 1931 a long period of cold wet weather in June killed many adults in the ground and made a decided gap in the collection of pollen. No other serious causes of mortality were noted.

The first males seen in the holes were found on July 13 and from that time on they were plentiful on flowers, showing that this was the beginning of the regular brood of males. Some of these may go back to the holes after emergence but as brood rearing continues long after this date, it is probable that they do not do so to any extent. None were ever noticed entering holes or hovering around them as some of the males of other species do. On the other hand, after rainstorms they were often found on flowers or leaves, stiff with cold and wet. When warmed up by the sun or in the hand they again became active. Some of them live until very late in the autumn; on October 3 several were collected on *Leontodon*, *Aster* and other flowers, together with females of the same species, and on October 6 an adult male, apparently just emerged, was taken from a hole together with two larvae. This last fact shows that brood rearing continues until late in the fall. In fact on October 3 many females were still taking pollen into their holes but this must have been due to the instinct of the insect to keep working as long as flowers are available and the temperature is not too low. Certainly pellets made at this time would not serve the purpose of rearing other bees.

The females apparently begin to construct hibernating quarters early in September, either by deepening the hole in which they were reared or by digging a new hole. At this time small cones of earth appear about the entrance of every hole. However they continue to go in and out of the hole and to visit flowers during fine warm weather until early October at least. As a rule many females hibernate together in the same hole. Males and females of this group were never seen *in copula*, but it is probable that mating takes

place on flowers, as the males do not have the habit of hovering about holes and nesting sites as do those of *H. leucozonius* or *H. rubicundus*. This species appears to have very little gregarious tendency, and holes were usually scattered all over any favorable spot. In some cases a particularly favored bank was found with a population of three to six holes per square foot over a small area, but these areas were always small.

6. *Andrena carlini* Ckll.

This bee seems to be partly colonial in habit; in some cases scattered holes were found, in others some dozens nested close together. They are, like all of the genus, entirely solitary, each female digging a hole, provisioning it, and laying an egg in each cell. There is only one generation per year, the females appearing early in spring and dying off about the middle of June or a little later.

The tunnels are made in light soil, often with gravel and small boulders in it, and usually among grasses or other vegetation. They are about $\frac{1}{8}$ in. in diameter, and often penetrate to a foot or more in depth, with many turns which make the total lengths much greater than this. The entrance to the hole is usually left open, but frequently becomes partly stopped by loose earth falling back from the rough mound left around the hole. The cells are at a distance of an inch or so from the main tunnel, and are provisioned with a mass of pollen and nectar. The connection between the tunnel and the cell is completely and firmly blocked with soil after the provisioning is done, making it difficult to tell just how many cells are present. The pollen mass is more nearly liquid than those of the *Halicti*. The cells were lined much as in that genus, but the tunnels seemed to be more roughly finished. The places where this bee nests are visited constantly by a species of *Nomada*, which undoubtedly is parasitic upon the *Andrena*. In some years cold wet weather also kills many of the adult females in the ground.

7. *Andrena wilkella* Kirby

Only a few nests of this species have been found, but they are apparently of the ordinary *Andrena* pattern. The bee appears in greatest numbers in areas having a heavy soil, and most of the nests found were in such localities. The character of the nest was quite different in different types of soil. In a light sandy loam a hole was followed to a depth of 18 in. while in clay the hole was seldom more than 6 or 8 in. The total length was always greater than the depth, because the holes of this species are very crooked. The entrance was always difficult to locate because it was invariably among dense low grasses, lichens, or other cover. A small quantity of earth was found about some holes; others had none. The cells are finished with the usual coating of fine clay, but the tunnels are not. After the cells have been provisioned with a pellet of pollen and nectar, the connection to the main tunnel is firmly packed with earth and a new cell made in another place. The young remain in this cell until they emerge in the following spring as adults.

Males of this species emerge considerably before the females and are often very numerous about apple trees and various shrubs, often when there are no flowers present at all. The females persist until long after apple bloom and have been seen as late as August 1 on clover. In England, the species is said to nest in large colonies, but all the holes found in Nova Scotia were scattered, although colonies may have been present in the district.

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TELIOSPORE DEVELOPMENT IN THE PUCCINIASTREAE[1]

By S. M. Pady[2]

Abstract

The genera that constitute the Pucciniastreae display a wide variation in the type of teliospore produced, as well as in the time and place of production. From the standpoint of development, however, there is a general situation that is common. In all genera primordial cells are formed from enlarged hyphal cells of the mycelium. These give rise to teliospore initials which are in the epidermal cells in *Calyptospora*, *Milesia*, *Hyalopsora* and *Thecopsora*, and are subepidermal in the other genera. These initials divide to form the mature teliospores, which are thick or thin walled, and few to many-celled. In all cases the teliospore is the product of a single primordial cell.

The teliospores of *Calyptospora goeppertiana* are formed from a perennial mycelium, which causes a witches' broom and hypertrophied stems on species of *Vaccinium*. The mycelium gives rise to primordial cells in the cortex just below the epidermis. Each primordial cell pierces the host wall above and the contents pass in to form the initial, which by growth and division becomes the teliospore. The mature teliospores are one- to four-celled, with a thickened, dark brown wall. Development is not simultaneous, but progressive, and the teliospores are first formed in the basal parts, moving slowly upward until every cell of the hypertrophied portion of the stem is completely filled. In four species of *Milesia* the method of development is similar. The spores, however, are thin walled, and are formed in the epidermal cells of the overwintered fronds of their fern hosts. *Thecopsora vacciniorum* is similar to *Milesia* in many respects. The teliospores are intra-epidermal, thin walled and multicellular. In *Pucciniastrum* the teliospores are subepidermal, and arise from primordial cells, as in *Calyptospora*, *Milesia* and *Thecopsora*. The teliospore initials are closely packed, and the mature spores may form extended crusts. The simplest type of development is found in *Uredinopsis*, which is generally considered to be the most primitive of the fern rusts. Primordial cells are formed in the same way as in the other genera. These round up to form the initials, and cross walls are laid down to give the mature spores.

From these studies two possible lines of development are suggested, both beginning with *Uredinopsis*. One line would lead through the intra-epidermal forms, as *Milesia*, *Calyptospora*, etc., and the other through the subepidermal genera, as *Pucciniastrum* and *Melampsoridium*.

Introduction

The Pucciniastreae constitute a subtribe of the Melampsoraceae, and are characterized by indehiscent telia and aecia of the peridermial type. The teliospores are intra-epidermal or subepidermal, and show a wide variation in time and place of development. In *Calyptospora*, *Milesia*, *Hyalopsora*, *Thecopsora* and *Melampsorella* the teliospores are formed in the epidermal cells, while in *Uredinopsis*, *Pucciniastrum* and *Melampsoridium* they are subepidermal. The general situation is shown in Table I.

From Table I it will be seen that there are considerable differences not only in the time of teliospore formation, but also in the position and in the type of spore produced. Little, however, has been known of the manner in which the teliospores develop in any of these genera. As Arthur (2, p. 149) has pointed

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TABLE I

TELIOSPORE FORMATION

Rust genus	Time	Place	Type of spore
Calyptospora	During the growing season	In epidermis of the stems	1-4 celled, thick walled
Milesia	Following spring*	In epidermis of over-wintered fronds	Multicellular, thin walled
Hyalopsora	Early spring	In epidermis of young fronds	Multicellular, thin walled
Thecopsora	At end of the growing season	In epidermis of season's leaves	Multicellular, thin walled
Uredinopsis	At end of the growing season	In mesophyll below epidermis	1-4 celled, or many celled, thin walled
Melampsoridium	At end of the growing season	Subepidermal	Single celled, thin walled
Pucciniastrum	At end of the growing season	Subepidermal	1-4 celled, thick walled

**In one species teliospores may also be formed at the end of the current season.*

out: "The development of the telial primordium in such genera as *Coleosporium*, *Melampsora*, *Melampsoropsis*, *Melampsorella*, *Uredinopsis*, *Milesia*, *Hyalopsora*, *Pucciniastrum*, in which the teliospores are sessile and arise under the cuticle or within or beneath the epidermis, has received little study." The following investigations were undertaken with the object of studying the method of teliospore development, especially in the genera in which the teliospores are intra-epidermal.

The species of Pucciniastreae that have been studied are parasitic on ferns and flowering plants, three genera, *Uredinopsis*, *Milesia* and *Hyalopsora*, being found on Pteridophytes, the remainder on Angiosperms. It might be noted here that with the exception of *Thecopsora vacciniorum*, the aecial host for all these species in eastern North America is *Abies balsamea*. The telial hosts are shown in Table II.

TABLE II

TELIAL HOSTS FOR SPECIES OF PUCCINIASTREAE

Rust species	Telial host
Calyptospora goeppertiana Kuhn	*Vaccinium pennsylvanicum* Lam. and *V. canadense* Kalm.
Milesia marginalis Faull and Watson	*Thelypteris marginalis* (L.) Nieuwl.
Milesia polypodophila (Bell) Faull	*Polypodium virginianum* L.
Milesia intermedia Faull	*Thelypteris spinulosa* var. *intermedia* (Muhl.) Weath.
Milesia fructuosa Faull	*Thelypteris spinulosa* var. *americana* (Fisch.) Weath.
Thecopsora vacciniorum (D.C.) Karst.	*Vaccinium pennsylvanicum* Lam. and *V. canadense* Kalm.
Melampsoridium betulinum (Pers.) Kleb.	*Betula pumila* L. (?)
Uredinopsis phegopteridis Arth.	*Thelypteris dryopteris* (L.) Slosson
Uredinopsis struthiopteridis Storm.	*Pteretis nodulosa* (Michx.) Nieuwl.
Pucciniastrum abieti-chamaenerii Kleb.	*Epilobium angustifolium* L.
Pucciniastrum epilobii (Pers.) Otth.	*Epilobium adenocaulon* Haussk.
Hyalopsora aspidiotus (Pk.) Magn.	*Thelypteris dryopteris* (L.) Slosson

Material and Methods

All the rusts described in this paper are found in abundance in the Temagami Forest Reserve in northern Ontario. The field laboratory of the Department of Botany, University of Toronto, is ideally situated in this region, and was used as a base for this work during the summers of 1930, 1931 and 1932. When material was brought into the laboratory it was placed in a moist chamber, and if freehand sections revealed the presence of desirable stages small portions were removed and placed in various fixatives. In a number of cases fixations were made in the field, especially where the particular collecting ground was located at some distance from the laboratory. Of the many fixatives that were tried, Flemming's weak has proved to be the best, although formalin-acetic-alcohol was successfully used in certain cases. The latter fixative is advantageous in that it also acts as a preservative, and material may be left in it for an indefinite period. Flemming's triple stain gave the best results and was used throughout. Heidenhain's hematoxylin was occasionally used to supplement the triple stain, but on the whole was rather unsatisfactory.

Freehand sections were employed with considerable success throughout these investigations. They not only served to reveal the presence of desirable stages in preliminary examination, but also proved to be valuable for comparison with stained microtome sections. Many of the drawings included in this paper have been made from freehand sections. Excellent results were obtained from fresh material following fixation in 95% alcohol, or in formalin-acetic-alcohol. Large quantities of selected material were placed in the latter where they were available for sectioning at any time. Freehand sections of preserved material may show an extraordinary amount of detail, especially when mounted in lactophenol which contains a small amount of cotton blue, or some other stain.

Species Investigated

1. *Calyptospora*

The genus *Calyptospora* was established by Kuhn (14) in 1869, with *C. goeppertiana* as the type species. The genus has remained monotypic though the combination *C. columnaris* (Alb. and Schw.) Kuhn is in more common use in America. Spermagonia and aecia were not known at the time, and the description was based entirely on the character of the teliospores, which were found to fill the epidermal cells of the stems of the host. Kuhn described the teliospores as irregular, ellipsoid, prismatic, obtuse above, rounded below, subfuscous, paler below; divided twice, or sometimes several times by cross walls. Mycelium was found to be distributed between the cells of the cortical tissue, causing an abnormal enlargement of the same. As a result, the stems of *Vaccinium vitis-idaea* became thickened and sponge-like all round, although enlargement was occasionally found only on one side.

Hartig (11) in addition to describing the hypertrophied stems, carried out infection experiments on *V. vitis-idaea*, and studied the development of the teliospores. Aeciospore infection gave rise to mycelium which established

itself in the cortex. The following year the new shoots were changed into the hypertrophied form. The mycelium grew into the new shoots, and caused an enlargement of the cortical cells, and this action was continued as long as the cells remained young. At the tip of the shoot, the cells were mature and thus were not stimulated to greater size. The intercellular hyphae derived their food from the parenchyma cells by means of haustoria. "The spores originate from processes of the mycelial hyphae which bore their way into the epidermal cells, and well up inside to form spherical sacs. The cells thus entered turn brown and are filled with four to eight cells produced from the sac-like process of the mycelium. From each cell of this kind a four-celled teleutospore is formed, and hibernates *in situ*" (translation). The infected stems became swollen to the size of a quill and were very conspicuous. This thickened spongy part of the stem was at first whitish or somewhat rosy in color, changing later to a brown or blackish brown color. Hartig's description was accompanied by three figures. The first showed a typical branch from a witches' broom with well-marked hypertrophied stems, the second dealt with the club-shaped bodies below the epidermal cells and the perforation of the cell wall, while in the third figure the teliospores, which have filled the epidermal cells, were shown to be germinating. Nuclear details were lacking in all figures.

Tubeuf (21) reviewed Hartig's work and added a more complete description of the hypertrophied twigs. "The mycelium hibernates in the cortical tissues, growing intercellularly and sending haustoria into the host cells. As a result of its presence growth is much accelerated, and a marked thickening of the attacked twigs frequently occurs; intercellular spaces become enlarged and the contents of all cortical cells, except those of the epidermis, take on a rose-red color, though they afterwards turn brown" (translation). Five figures accompanied the description, three of which were the figures of Hartig, described above.

Grove (10) has given an account of the infected stems, which he found to be swollen and clear pink at first, later becoming brown. The teliospores were described as caulicolous, developed in the epidermal cells, densely-crowded, prismatic, mostly divided by crossed longitudinal walls into four cells, up to 48μ high, epispore yellowish-brown, smooth, thickened (up to 3μ) at the summit, with a germ pore at the upper and inner corner of each cell. The teliospores were formed in the stems of *Vaccinium vitis-idaea* during July and August in England and in Wales.

Sydow (20) in his Monographia Uredinearum, has given an excellent review of the earlier work. His description of the teliospores was also very complete.

The purpose of this investigation was to study the development of these intradermal teliospores. What is the nature of the sac-like bodies described by Hartig? How many are formed per epidermal cell? How many teliospores are developed from one sac-like body? These are some of the questions this investigation has sought to answer.

Calyptospora goeppertiana is found in abundance in the Temagami region on *Vaccinium pennsylvanicum* and *V. canadense*. The fungus stimulates the host, resulting in excessive branching, and this gives the affected plant its witches' broom appearance, which is accentuated by the marked hypertrophy of the stems. The infected branches of the previous year are greatly hypertrophied, being three to four times the diameter of a normal branch, dark brown in color, corky in consistency and quite dead. In the spring a large number of new shoots appear from the base of these dead branches, and these are soon invaded by the perennial mycelium. The young infected shoots may readily be distinguished from normal shoots by their slightly larger size, pale green color, and soft fleshy appearance.

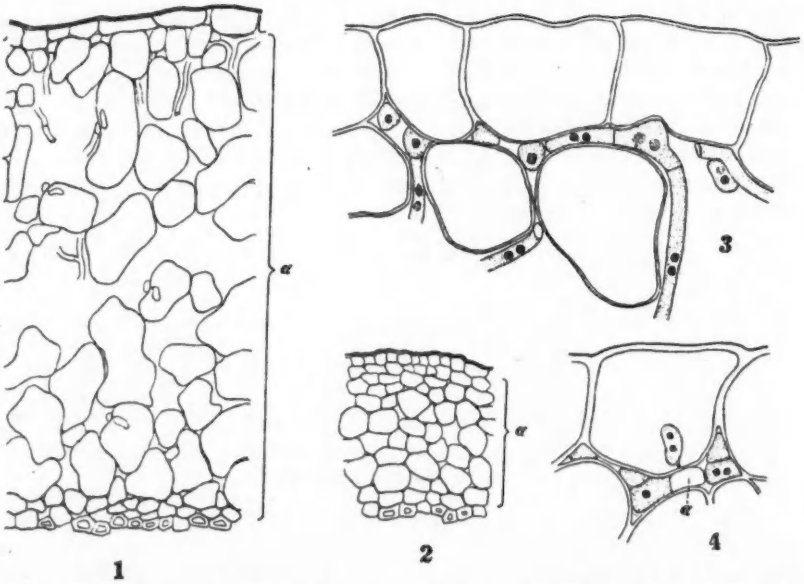

FIG. 1–4. *Calyptospora goeppertiana.* FIG. 1. *Cross section of hypertophied stem showing portion of cortex (a).* × *120.* FIG. 2. *Cross section of normal stem with only cortex (a) shown.* × *120.* FIG. 3. *Early stage. Mycelium aggregating below epidermis.* × *750.* FIG. 4. *Another view of the same stage. Note the haustorium and haustorial mother cell (a).* × *750.*

The infected shoots continue their growth and reach a considerable length. The hypertrophied areas become more and more prominent, increasing in length as the shoot elongates, and also increasing in diameter until they reach a size three to four times that of the normal shoots. This is illustrated in Figs. 1 and 2. Fig. 1 shows a cross section of an infected stem, the cortex *(a)* only being drawn. Fig. 2 shows a corresponding section through the cortex *(a)* of a normal uninfected stem. It will be observed that the cortex in Fig. 1 is more than three times greater in thickness than the cortex of Fig. 2.

The mycelium grows rapidly through the intercellular spaces of the cortex and a section through the stem at this stage reveals the presence of mycelium in the large intercellular spaces, and abundant haustoria in the cells. The next change that may be observed is that the hyphae appear to grow outward, and become aggregated just below the cells of the epidermis (Fig. 3). Haustoria are found not only in the cortical cells, but also in the epidermis (Fig. 4). The haustorium in this figure has been formed from the haustorial mother cell *(a)* which is about the same size as the adjacent hyphal cells massed in the intercellular spaces just below the epidermal cells. The hyphal cells that lie in close contact with the epidermis now commence to increase very rapidly in size, and this is apparently the first step in the formation of the teliospores. These enlarged hyphal cells become the primordial cells, and this stage will be referred to as the primordial stage.

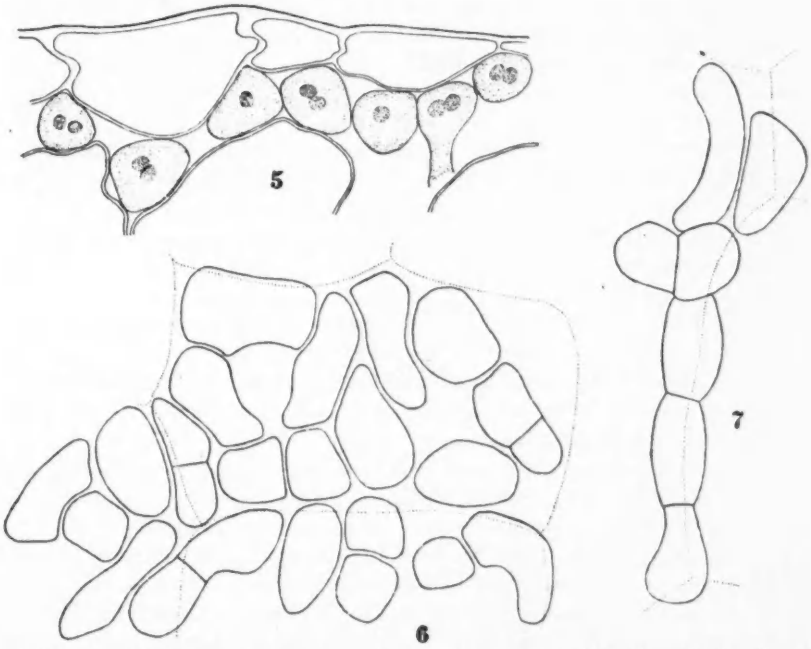

FIG. 5–7. *Calyptospora goeppertiana.* FIG. 5. *Young primordial cells.* ×750. FIG. 6. *Surface view of primordial cells. Walls of epidermal cell indicated by dotted lines.* × 840. FIG. 7. *Young primordial cells at the junction of two epidermal cells.* × 840.

The young primordial cells form a loosely arranged layer just below the epidermis (Fig. 5). They are typically binucleate and densely filled with contents, which shows such a strong affinity for the stain that the nuclei are often obscured. The nature of this loosely arranged irregular primordial layer is best shown from a surface view, as in Fig. 6. The material from which this drawing was made was obtained by stripping the epidermis from a

freshly collected plant, immersing it in 95% alcohol for a few seconds, and then mounting directly in lactophenol to which a small quantity of cotton blue had been added. The primordial cells stain very deeply and their dark blue color stands out in sharp contrast to the colorless epidermal cells above. There is a considerable variation in the shape and size of the cells shown in this figure, the majority being very irregular and ranging in size from 12-22 μ in length to 8-17 μ in width. A favorite position for the massing of the hyphae, and thus for the formation of primordial cells, is in the intercellular space which lies below the junction of two epidermal cells. In many cases a hyphal strand forces its way through this intercellular space following the outline of the epidermal cells. Each cell of this runner may now enlarge and a row of primordial cells may be formed below the common wall of the overlying epidermal cells (Fig. 7). The primordial cells are not restricted to these intercellular spaces, and may "cover" the underportion of the epidermal cell wall more or less completely (Fig. 6). In this figure 13 primordial cells may be found below the single epidermal cell, the outlines of which are represented by the dotted lines. The number of primordial cells per epidermal cell varies, in some cases there being very few. Where they occur singly they are somewhat oval or club-shaped and possess a fairly regular outline (Fig. 8). The two isolated primordial cells are typical of this stage and show the two characteristic nuclei as well as the dense cytoplasmic contents.

The primordial cell stage is marked externally by a change in the appearance of the hypertrophied stems, which now lose their pale green color and become rose or flesh colored. Earlier workers, as Hartig and Tubeuf, had called attention to this peculiar flesh-colored character, but it had never been correlated in any way with the development of the parasite. As the hyphae mass up under the epidermis and the primordial cells begin to develop, the contents of the epidermal cells begins to disintegrate, and the pale green color of the stem disappears.

The contents of the primordial cells now begins to pass into the cells of the epidermis. The epidermal cell wall which overlies the primordial cell is pierced, and a small opening is formed immediately above the primordial cell through which the contents passes into the interior. These openings are very minute and it is difficult to observe them in this stage, although they may be found very readily in horizontal sections through mature spores. In cross section they appear as small white spots in the epidermal cell wall. As the cytoplasm passes through, a small globular body is formed directly on the cell wall. The youngest stages that have been found are small heavily staining bodies in the epidermal cell (Fig. 9, *a*, *b;* Fig. 10, *a*). These are called teliospore initials, since each one grows directly into a teliospore. As the initial increases in size (Fig. 9, *c*, *d*, *e*) the two nuclei move to the opening and pass through along with the remaining cytoplasm (Fig. 10, *b*).

Each primordial cell gives rise to a single teliospore initial and thus the number of teliospore initials in a single epidermal cell depends upon the number of primordial cells that are formed below it. Where the number is

small, the initials tend to retain their globular shape (Fig. 9, *b*, *d*; Fig. 10, *b*), but where many are developing in the same cell, the initials become crowded and are somewhat sac-like or elongated (Fig. 10, *c*). It was this sac-like appearance that led to much confusion in earlier studies of *Calyptospora*. In this stage the initials often resemble haustoria, and as haustoria are normally present in the epidermal cells (Fig. 9, *f*; Fig. 10, *d*, *e*), they were at first thought to be the initials themselves. That this is clearly not the case is shown when the initials are compared with the haustoria. A typical haustorium possesses a well-marked, peg-like process, at the end of which is located the narrow sac-like haustorium (Fig. 11).

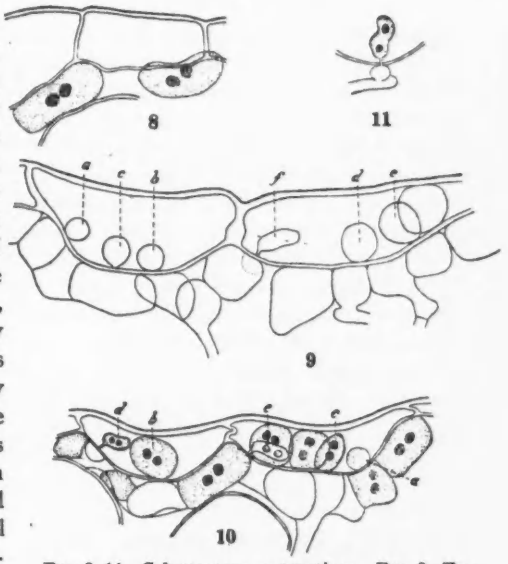

FIG. 8–11. *Calyptospora goeppertiana*. FIG. 8. *Two primordial cells.* ×620. FIG. 9. *Teliospore initials at a, b, c, d, e. Haustorium at f.* × 620. FIG. 10. *Teliospore initials a, b. c. Haustoria at e, f.* ×620. FIG. 11. *Typical haustorium from cortex.* × 620.

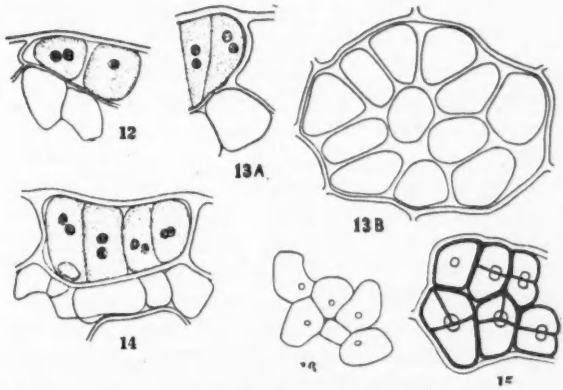

FIG. 12–16. *Calyptospora goeppertiana*. FIG. 12. *Two teliospore initials. Note the empty primordial cells below.* × 540. FIG. 13A. *Slightly later stage with opening in the cell wall just above the empty primordial cell.* × 630. FIG. 13B. *Surface view of a single epidermal cell containing 12 teliospore initials.* × 540. FIG. 14. *Cross section of later stage showing an epidermal cell almost completely filled.* × 540. FIG. 15. *Mature teliospores in epidermis showing thickened walls and germ pores.* × 540. FIG. 16. *Group of empty primordial cells showing the opening through which the teliospore initials have arisen.* × 540.

The teliospore initial, on the other hand, is spherical, seated directly on the cell wall, and appears to arise without any suggestion of a penetration peg.

The teliospore initials increase in size, flattening out against the upper and lower walls of the epidermal cell. The cytoplasm is distinctly vacuolate, the two nuclei are close together and the whole initial is in striking contrast to the large empty primordial cell below (Fig. 12). A surface view of this stage shows that the epidermal

cell becomes more or less filled with these large teliospore initials, which lose their rounded appearance as they conform to the shape of the host cell, and as they become flattened against their neighbors (Fig. 13, B). In this figure 12 teliospore initials may be observed in a single epidermal cell. As further increase in size takes place the nuclei divide conjugately, a cross wall is laid down, and the initial becomes two celled. The opening in the cell wall through which the contents of the primordial cell has passed may occasionally be observed (Fig. 13, A). In Fig. 14 two initials are shown in cross section, and the epidermal cell is more or less completely filled. A number of empty primordial cells may still be observed below this cell of the epidermis, while a small haustorium is discernible at the lower left-hand corner of the cell.

The initials which have divided, or are about to divide, are more properly termed young teliospores, since they may become teliospores without further division. The initial may not even divide but may grow directly into a single-celled spore. In most cases, however, division does take place, and as a result the teliospores are two, three or four-celled. As the spores mature the walls become thickened and dark brown in color. Of the six mature teliospores shown in the surface view in Fig. 15, it will be seen that one is single celled, three are two celled and two are three celled. The germ pores are characteristic, in the two-celled spores occupying a central position on the upper wall, one on each side of the cross wall, and in the three- and four-celled spores they are situated in the upper and inner corner. Each cell contains a fusion nucleus, which is in the resting condition. Below the epidermis the large empty primordial cells can readily be seen, each with a small opening through which the contents has passed into the teliospore initials (Fig. 16).

The number of teliospores contained in a single epidermal cell depends, of course, upon the number of teliospore initials. In Fig. 13 are found 12 initials, which indicates that in this epidermal cell 12 teliospores would be developed. The number of initials depends also upon the number of primordial cells. Below the epidermal cell shown in Fig. 6, 13 primordial cells may be counted. Although the number appears to vary somewhat, it seems that on the average about 12 primordial cells are formed to each epidermal cell, and thus 12 teliospores at the time of maturity.

One of the most striking features of teliospore development is that it is not simultaneous, but begins at the base of the stem and progresses steadily upward. As the teliospores mature the thickened walls give the infected stems a golden brown color, which deepens later so that the stems have a varnished, dark brown appearance. Above this is a narrow light brown zone, which is characterized by the presence of young teliospore initials. The stem, just above this light brown area, possesses the rose color characteristic of the young infected stems, and which we find in the primordial stage referred to previously. Thus, the formation of teliospores in *Calyptospora* is progressive, and there are three zones or areas on the stem; the lower part containing mature spores and dark brown in color; the intermediate zone where

teliospore initials are present, which is light brown in color; the upper part in the primordial stage, and flesh or rose in color. The extent of this intermediate zone is somewhat variable, but is usually rather short. One typical infected twig in this condition was measured; the hypertrophied length was found to be 50 cm., the dark brown area measured 32 cm., the light brown area 8 cm., and the upper portion in the primordial stage 10 cm.

Hartig (11) in his description of the development of the teliospores, indicated quite clearly the massing of the mycelium beneath the epidermal cells where certain hyphae became thickened in a club-shaped manner (see his Fig. 122, *a*, *a*). These are undoubtedly primordial cells, although they are much smaller than those found by the writer. Hartig has also shown in this figure the presence of haustoria and young teliospore mother cells in the epidermal cells. A slightly later stage *(c)* was shown in one case which corresponds closely with the teliospore initials described above. The teliospore mother cells were thought by Hartig to divide into four teliospores. If the teliospore mother cells of Hartig are considered to be teliospore initials, then the four teliospores are the result of the division of this initial, and are simply the four cells of a single teliospore. From the standpoint of development a teliospore is the product of a teliospore initial regardless of whether the initial divides many times or not at all. In *Calyptospora* the initials usually divide but the teliospores have not been found to exceed more than four cells.

2. *Milesia*

Among the genera that are included in the Pucciniastreae are three which comprise the common fern rusts of temperate regions, namely *Milesia*, *Hyalopsora* and *Uredinopsis*. Although Moss (16) has studied the uredo stage of these genera, very little is known of the development of the teliospores. The results of investigations made in this connection on *Hyalopsora* are being described in a separate paper (18), while the studies that have been made upon *Uredinopsis* will be described later in this paper. It is with the genus *Milesia* that the writer is at present concerned. In a recent monograph of this genus, Faull (6) has discussed the taxonomy and geographical distribution, and has also reviewed the investigations of earlier workers. In his discussion of the taxonomy Faull has concluded that *Milesia* White should be the proper name for the genus, and *M. polypodii* White the type species. In this paper the generic name will be used as defined by Faull.

The teliospores of *Milesia* are intradermal, as in *Calyptospora*, but in this case the spores are formed in the epidermal cells of the old overwintered fronds. Earlier workers looked for teliospores during the current season, and considered them to be of rare occurrence. The explanation is that in most cases they were entirely overlooked. As Faull has pointed out, "this is not surprising, because they bear little resemblance to spores, and until one knows when and where to look for them they are not likely to be seen." In his monograph covering 33 species, teliospores are described for 22 species and varieties. Kamei (12), in a note on *Milesina vogesiaca*, has given two

figures of the mature teliospores. One figure was a cross section through two epidermal cells showing the intradermal teliospores and below the epidermis, mycelium with a few small empty rounded hyphal cells. In a later paper (13) Kamei described and figured a new species, *M. jezoensis*, in which the same type of cell was shown beneath the epidermis.

In the Lake Temagami region where the species included in this paper were collected and studied, there appear to be four species of *Milesia: M. marginalis*, whose teliospores develop in the spring on the overwintered fronds of *Thelypteris marginalis; M. polypodophila* and *M. intermedia*, which are similar in time of development, and which are found on *Polypodium virginianum* and *Thelypteris spinulosa intermedia* respectively; the fourth species, *M. fructuosa*, is found in the fall on the season's leaves of *Thelypteris spinulosa americana*. Although the bases on which *M. fructuosa* and *M. intermedia* have been separated might be open to question, they will be referred to in this paper as acceptable species. The development of the teliospores has been studied in all four species and the results indicate that there is a striking similarity in the manner of development in all of them. It was accordingly thought best to illustrate the manner of development by reference to only one species, and *M. marginalis* was therefore selected for detailed study. Such differences as may have been found in the other species will be indicated in the course of the paper.

The appearance of the infected parts of the overwintered fronds in which the teliospores will be formed is very characteristic. In *M. marginalis* these infected patches are usually light brown or tan in color, and extend over a considerable area. There is also much variation in the size of these light brown patches, from small limited portions to areas involving half the pinnule. A peculiar feature is that infection is often found on only one side of the main vein, although basal infections are sometimes extended over both sides. The usual appearance, however, is a well-defined light brown area of varying size on either side of the main vein. There is also considerable physiological browning, which tends to obscure the areas of infection. This type of browning is usually not localized but involves a number of pinnules.

In *Milesia polypodophila*, the infected leaves show dark brown localized patches at the margins or tips of the pinnae. The epidermis usually becomes separated from the cells below, and may be readily stripped off. Whether this is due entirely to the rust mycelium or to senescence of the leaf, or both, has not been determined. As in *M. marginalis*, there is often considerable browning that is not due to the rust infection, and which tends to obscure the part of the leaf in which teliospores are developing. In this connection the presence of uredinial pustules was a valuable aid in discovering these areas, due to the fact that they are usually found in association with the teliospores. In *M. intermedia*, on the other hand, the uredinia rarely have been found. The lesions in which the teliospores are produced are rather extensive in this species, and are brown in color. *Milesia fructuosa* causes large dark blotches on the fronds, which may extend over several pinnules.

Sections through these infected areas indicate the presence of abundant mycelium throughout the intercellular spaces of the mesophyll. The mycelium is composed of rather large hyphal cells, each with two nuclei. The first indication of the beginning of teliospore formation is in the aggregation of hyphae below the epidermal cells. This phase is not as prominent as in *Calyptospora*, where a great many hyphae are massed below the epidermis. In *M. marginalis* fewer hyphae take part in the process, while occasionally only a single mycelial strand is found.

The formation of primordial cells in all *Milesia* species is similar in every way to the process described earlier for *Calyptospora*. The simplest type is where a hyphal tip becomes greatly enlarged and is cut off to form the primordial cell. More often, however, the origin of the primordial cells is from a hyphal runner, which is applied closely to the epidermis (Fig. 17). In the hyphal runner shown in this figure the cell at the tip has become cut off to form a primordial cell, while the cells of the strand are much enlarged, and will undoubtedly break up into other primordial cells. Two branches are given off this runner immediately below the side walls of the overlying epidermal cell. When the epidermis is stripped off, the primordial cells are often found in this position, indicating that they have arisen from such hyphal runners.

The mature primordial cells are typically binucleate and filled with cytoplasm, which is usually vacuolate (Fig. 18). The nuclei are very prominent, owing chiefly to the presence of a single large nucleolus. The primordial cells are larger than in *Calyptospora*, and often have a length of 28 μ and a width of 15 μ, occasionally being even larger.

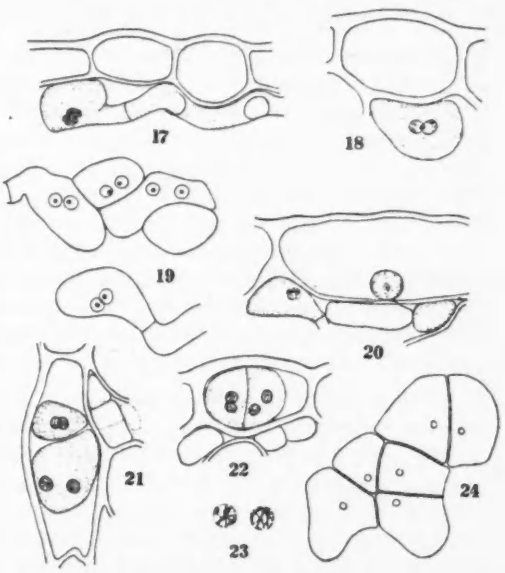

FIG. 17–24. *Milesia marginalis. All figures* × *600.* FIG. 17. *Hyphal runner below lower epidermis. Individual cells much enlarged and the tip rounded up to form a primordial cell.* FIG. 18. *Cross section through an epidermal cell with a mature primordial cell below.* FIG. 19. *Surface view of a group of primordial cells. The four upper cells are somewhat irregular in shape, while the single one just below is club-shaped.* FIG. 20. *A young teliospore initial arising from the central primordial cell.* FIG. 21. *Two initials, the lower one being much larger. Note the empty primordial cells in the small intercellular space just below the epidermal cell.* FIG. 22. *Two-celled stage.* FIG. 23. *Two fusion nuclei from two cells of a mature teliospore.* FIG. 24. *A mature teliospore with six cells, whose shape corresponds to that of the epidermal cell. A germ pore is present on the upper wall of each cell.*

Single primordial cells are somewhat club-shaped and are applied closely to the epidermis (Fig. 18). Where the primordial cells occur in groups they are somewhat smaller in size and are usually irregular in shape. This is well illustrated in Fig. 19, which is a surface view of a group of five primordial cells. The upper four tend to be somewhat irregular, while the lower single one is regular and club-shaped.

In *Milesia marginalis* the primordial cells are formed more abundantly beneath the cells of the lower epidermis, than below the upper epidermis. The cells of the mesophyll are more compact in the upper part of the leaf, and the intercellular spaces are less abundant and often much smaller. The primordial cells, as a result, are very irregular in shape and much smaller in size. This characteristic of conforming to the shape and size of the intercellular space has been found to be true of *Hyalopsora* (18), and is probably found in all species which possess intradermal teliospores.

The number of primordial cells produced is not large. When the epidermis is stripped off small groups can be found, with here and there single cells. Since the number of teliospores is proportional to the number of primordial cells, the number of epidermal cells containing teliospores should give some clue to the number of primordial cells produced. In a surface of 15 epidermal cells 13 were found to contain teliospores, and two were empty. Of these 13, one cell contained four teliospores and was completely filled, while in the remaining 12 there were from one to three spores which filled only part of the epidermal cell. Thus, in the 15 epidermal cells there were approximately 22 teliospores, which indicates the presence of 22 primordial cells. The number of teliospores per epidermal cell however varies greatly, and a single epidermal cell may have as many as five or six, or may have but a single one.

In *Milesia intermedia* the primordial cells are much smaller, and there is a tendency for them to become somewhat irregular. *Milesia polypodophila*, on the other hand, possesses primordial cells which agree very closely with the description given for *M. marginalis*. The primordial cells of *M. fructuosa* are somewhat different from the other species. They are much elongated and usually very narrow. Where they are crowded by the host cells they conform to the shape of the intercellular space, and may be much smaller. In all cases, however, two nuclei are present and the contents is filled with dense cytoplasm.

The passage of the contents from the primordial cell into the host and the formation of teliospore initials have been studied in all four species. The first indication of this process is seen in the formation of small round globular structures in the epidermal cell immediately above the primordial cells. As the contents passes in, these globular bodies increase rapidly in size and it is very difficult to find the first stages. Fig. 20 is an early stage of *M. marginalis* showing three primordial cells and a teliospore initial in the epidermis which has arisen from the central one. Much of the cytoplasm has already passed in and the initial has stained so deeply that it is impossible to make out the

nuclei. These stages have been observed in the other three species, and they agree very closely with *M. marginalis*. *Milesia fructuosa* is especially favorable for the study of the early stages of the teliospore initials.

The young teliospore initial grows rapidly as the contents flows in, and assumes a spherical or slightly oval shape. Where two or three are growing side by side there is usually considerable crowding and the shape of the initial is often altered. In Fig. 21 two initials are shown, the upper one of which is filled with contents and stains very heavily, while the lower is much older and the cytoplasm is vacuolate. In both there is a slight tapering toward the base. This tapering in *M. intermedia* is found even where there is but a single initial in the cell. The nuclei in the teliospore initial now divide, and we have a two-celled stage, each cell with two prominent nuclei (Fig. 22). Further division takes place resulting in the formation of many-celled teliospores, completely filling the epidermal cell. Since these spores conform to the shape of the epidermal cell, and also to the presence of neighboring spores, it becomes very difficult to distinguish just how many cells belong to a particular spore. According to Sydow (20) it is not easy to determine the exact size and extent of the single spores. In some cells of the epidermis there appear to be four cells in isolated groups, each group being the result of two divisions of the teliospore initial. In other cases the number of cells is much greater. This may be due to the presence of more than one primordial cell or to a greater number of divisions of the teliospore initial. The final result is that the epidermal cell becomes filled with multicellular thin-walled teliospores, which conform to the shape of the epidermal cell, completely filling it. Below the epidermal cells the empty primordial cells may be found. Kamei's figures are of this stage and his empty hyphal cells are undoubtedly empty primordial cells.

Each cell of the teliospore contains two nuclei, each with a prominent nucleolus. As the teliospores mature, the two nuclei approach each other and a large fusion nucleus results. The details of the nuclear fusion have not been studied, but the following stages may be noted. In *M. fructuosa* the fusion nucleus immediately goes into a resting condition, the chromatin being in the form of very fine granules, and the whole nucleus has a homogeneous appearance. The two nucleoli do not fuse immediately, and both are present in the resting stage, which is of brief duration. A spireme thread is evolved, and sections through mature teliospores indicate quite clearly that the fusion nucleus is not in a resting condition, but is always found in prophase. Two typical fusion nuclei are shown in Fig. 23. In the nucleus at the left a single large nucleolus is present, which is probably the result of fusion. In all four species of *Milesia* the fusion nucleus of the mature teliospore has been found to be in this spireme stage.

In a separate paper (18) attention has been drawn to the nuclear condition in the teliospores of *Hyalopsora aspidiotus*. The nuclei came together and immediately passed into a short resting period. The fusion nucleus then entered into heterotypic prophase, and a well-defined spireme was evolved

which was shown to be double. The nuclei of the mature spores were therefore in an advanced stage of prophase, and not in a resting condition. This stage was of long duration, as the remaining stages took place in the promycelium when the spores germinated. Although all the stages have not been observed in *Milesia*, the number that have been found are sufficient to indicate that we have a situation in *Milesia* which is comparable in every way with *H. aspidiotus*.

Each cell of a teliospore possesses a well-marked germ pore. In Fig. 24 a single teliospore is shown in surface view, which is composed of irregular cells, each with a germ pore in the upper wall. This group of cells conforms to the general shape of the containing epidermal cell, which is not indicated in the drawing. A comparison of this figure with Fig. 15 of *Calyptospora* indicates quite clearly the difference in spore structure and in germ pores. In *C. goeppertiana* the teliospores are thick walled and germinate the following spring; in *Milesia*, as in *Hyalopsora*, they are thin walled and germinate at once. The germ pores of *Calyptospora*, which are located at the upper and inner corner of each cell, indicate their origin from a teliospore initial. In *Milesia*, however, the germ pores are located on the upper wall, but at no particular point in so far as the teliospore initial is concerned.

3. *Thecopsora*

Thecopsora vacciniorum occurs on the leaves of *Vaccinium pennsylvanicum* and *V. canadense*. It is found fairly abundantly on the under side of the leaves as small whitish spots, which become brown as the teliospores mature. At Lake Temagami in northern Ontario, where this rust was studied, the teliospores begin to develop toward the end of the growing season, and all stages may be found during September. The teliospores are intradermal and are found in both the upper and lower epidermis. This character led Magnus to separate from *Pucciniastrum* all those species whose teliospores are not subepidermal, but are found in the epidermis, and on this basis he created a new genus, *Thecopsora*. Dietel (4) in his recent treatment of the Uredinales, has retained this generic name, and has brought together all the genera whose teliospores are borne in the epidermal cells. This grouping includes *Calyptospora*, *Milesia*, *Hyalopsora* and *Thecopsora*, all of which have been studied from the standpoint of teliospore development. It has been found that *Thecopsora* is similar to the above three genera in the manner in which the teliospores are formed. From the standpoint of development, it would seem that *Thecopsora* should be separated from *Pucciniastrum*, and the generic name has accordingly been used throughout this paper.

During the growing season the rust is present in the uredinial stage and the mycelium becomes well established in the leaf. In September the primordial cells are formed and from them the teliospores are developed. The palisade layer is very compact and intercellular spaces are not abundant, while the loosely arranged mesophyll beneath the lower epidermis, on the other hand, is provided with a great many air spaces. It is in these spaces between palisade cells or between cells of the mesophyll that primordial cells are developed.

The first indication that can be found of primordial cell development is the slight enlargement of hyphal cells in the intercellular spaces just below the epidermis. These enlargements are not as prominent as in *Milesia* or *Calyptospora*, since the mycelium in the leaf is composed of rather large hyphal cells, which do not differ greatly from young primordial cells.

The mycelium is most abundant in the mesophyll, where the intercellular spaces are large. In order to reach the upper epidermis, the hyphae force their way between the palisade cells, and when the epidermis is reached they flatten out against the wall of the epidermal cell, the whole tip expanding slightly, conforming to the intercellular space. The cytoplasm becomes very dense and two nuclei are regularly present (Fig. 25). This type of primordial cell is found only when the tissues of the host are very compact. Below the lower epidermis certain hyphal cells, in many instances the end cell of a mycelial strand, enlarge to form small irregular binucleate primordial cells (Fig. 26). A comparison of Figs. 25 and 26 illustrates quite clearly the two different types of primordial cells, and also gives some indication of the difference between the structure of the upper and lower epidermis.

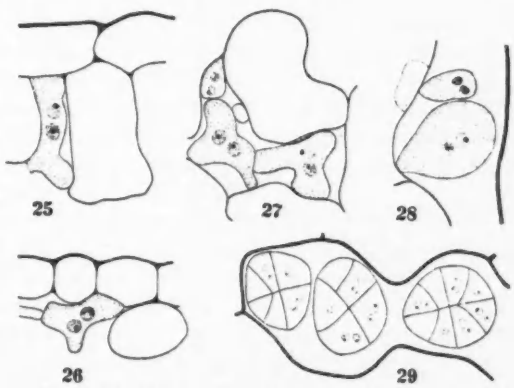

FIG. 25–29. *Thecopsora vacciniorum. All figures × 610.* FIG. 25. *A primordial cell below the upper epidermis.* FIG. 26. *Primordial cell beneath lower epidermis. Note the difference in shape when the primordial cell lies in a large intercellular space.* FIG. 27. *Two characteristic primordial cells in an intercellular space in the mesophyll immediately beneath the lower epidermis, shown in cross section.* FIG. 28. *Two teliospore initials in a cell of the upper epidermis. The smaller initial is densely filled with cytoplasm. The initial just below is a later stage.* FIG. 29. *Surface view of a part of a cell of the upper epidermis, containing three multicellular teliospores.*

The number of primordial cells that are formed is not large. Horizontal sections through the infected areas indicate that the number of primordial cells per epidermal cell is usually small. This is especially true of the upper epidermis where the number is small in comparison with the lower epidermis, where they are much more abundant. Two typical primordial cells are shown in Fig. 27, which is a horizontal section through the mesophyll beneath the lower epidermis. Mature primordial cells are filled with contents which show a strong affinity for stain, and these are always binucleate, each nucleus having a prominent nucleolus.

The contents of the primordial cell now passes through the lower wall of the epidermal cell, the passage of the contents taking place very rapidly, as in *Milesia* and *Hyalopsora*. The youngest stage that could be found is shown in Fig. 28, which illustrates two teliospore initials. The upper one is small

sac-like and binucleate, with dense contents which has just passed in from the primordial cell. Increase in size takes place and the teliospore initial becomes greatly enlarged. In the upper epidermis the initial becomes somewhat obovate in shape (Fig. 28), while in the lower epidermis the cells are much smaller and the initial soon conforms to the shape of the host cell. The cytoplasm is very vacuolate and the two nuclei are prominent.

The nuclei in the teliospore initial begin to divide and vertical septations are laid down, giving a multicellular teliospore. The first two septations are usually at right angles to each other and divide the initial into four cells. Where the cross walls meet at the centre of the spore, there is usually a well-defined polar furrow. These septations, however, do not necessarily divide the initial in a symmetrical manner, and the spore may have a very irregular appearance. This is especially marked in the teliospores that are formed in the lower epidermis where the cells are much smaller and narrower than those of the upper epidermis, and the initials during growth conform to the adjacent cell walls so that the mature teliospores are very irregular, often filling the cells. Where there are fewer initials in a cell, and where spacial relations permit, the teliospore tends to retain a definite outline.

In the larger cells of the upper epidermis there is sufficient room for the teliospore initials to develop, and the teliospores have a rounded outline. Since the initials are few in number, the teliospores of the upper epidermis are scattered, or in small irregular groups. In 19 epidermal cells examined six possessed a single teliospore; in nine others there were two, in two there were three, while the two remaining cells each contained four teliospores. As the spores mature, septations are laid down in a very irregular fashion. Three typical teliospores from the upper epidermis are shown in Fig. 29. The spore at the left contains six cells, the central one five, while the spore at the right is eight celled, and is bilaterally symmetrical. In any group of spores from the lower epidermis there is a greater variation in shape, size and number of septations. Two nuclei are present in each cell of the teliospore. These nuclei probably fuse later, although fusion has not been observed.

4. *Pucciniastrum*

In the Temagami region of northern Ontario a number of species of *Pucciniastrum* have been found. Of special interest are five species, namely, *P. abieti-chamaenerii*, *P. epilobii*, *P. pyrolae*, *P. potentillae* and *P. agrimonae*. Two other species are present in abundance, *P. americanum* and *P. arcticum*. Teliospores were found in only four of the above seven species. These four species have been studied and it has been found that *P. epilobii*, *P. americanum* and *P. arcticum* are very similar in the method of teliospore development, while *P. abieti-chamaenerii* differs from all three. As a result, *P. abieti-chamaenerii* and *P. epilobii* have been selected as representative and will be described in detail.

Pucciniastrum abieti-chamaenerii is found on *Epilobium angustifolium*, while *P. epilobii* occurs on *E. adenocaulon*. The teliospores of both species are formed late in the growing season, and collections were made during

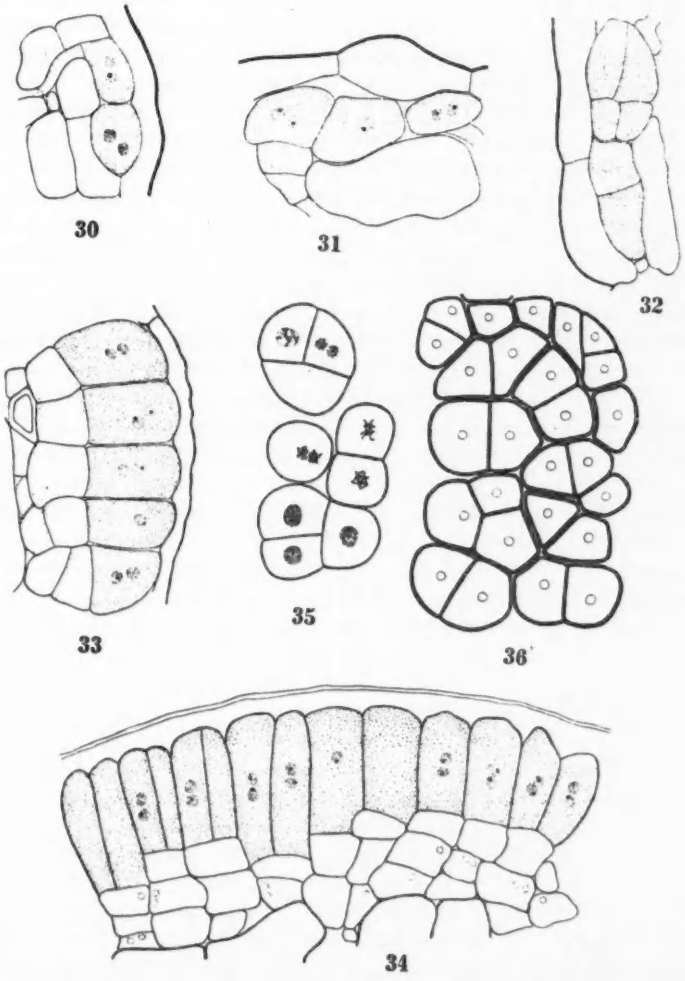

FIG. 30–36. *Pucciniastrum. All figures × 720.* FIG. 30. *P. epilobii. Two young primordial cells below the epidermis, which is indicated by a heavier line.* FIGS. 31–34. *P. abieti-chamaenerii.* FIG. 31. *A median section through a group of primordial cells.* FIG. 32. *Four primordial cells, the upper two of which have undergone division.* FIG. 33. *Later stage showing growth in a vertical direction, and also empty basal cells.* FIG. 34. *A section through a group of teliospore initials, which are the terminal cells of a vertical row. Five of the initials have divided, laying down vertical septations. All cells, except the teliospore initials, are practically empty.* FIG. 35. *P. epilobii. A horizontal section through a number of teliospores, showing different nuclear conditions at the time of fusion. The mature teliospores have a single fusion nucleus.* FIG. 36. *P. abieti-chamaenerii. Horizontal view of the edge of a large group of mature teliospores with thick cell walls and germ pores.*

September and October. In *P. abieti-chamaenerii* they form extensive crusts which appear on the under side of the leaves as blackish-brown areas. The teliospore layer in *P. epilobii* is much smaller. The mature teliospores, which are well described by Sydow (20), are thick walled and are always subepidermal, and in this respect differ from the teliospores of *Calyptospora*, *Milesia* and *Thecopsora*, which are intra-epidermal. From the standpoint of development also, *Pucciniastrum* has been found to be considerably different.

During the growing season the mycelium is well developed, and often fills the intercellular spaces of the leaf. Toward the end of August sections through infected parts of the leaf indicate that certain hyphae force their way between the cells of the mesophyll just beneath the lower epidermis. The tissues in the *Epilobium* leaf are very compact and the hyphae, in growing toward the epidermis, separate the mesophyll cells as they grow between them. When they reach the lower epidermis, they tend to flatten out against the lower wall. The end cell of the hypha becomes cut off and begins to increase in size. Fig. 30 shows two very young primordial cells of *P. epilobii*, the upper one being the terminal cell of the hyphal strand. As growth takes place the epidermis becomes slightly raised. The contents of the primordial cells stains very deeply and it is difficult to make out the details of the two nuclei which are present.

In *Pucciniastrum abieti-chamaenerii* the primordial cells are formed in a somewhat similar fashion, except that a great many hyphae are involved, and the formation of primordial cells is not necessarily a property of the terminal hyphal cells. While in a few cases primordial cells are solitary or in a small group, in most cases a great many are formed from a hyphal complex just beneath the lower epidermis. Fig. 31 is a section through the middle of a group of primordial cells in various stages of development. On either side of this median section are other primordial cells, which are smaller toward the outer edge of the group. It is clear that these have arisen from a weft of hyphae, a few strands of which may still be seen. At the centre of the group the cells are large and closely packed, while toward the edge they tend to be smaller and more diffuse. The mature primordial cells of *P. abieti-chamaenerii* may reach a considerable size (Fig. 31) as compared with those of *P. epilobii* (Fig. 30). In both species, however, the primordial cells consist of enlarged thin-walled binucleate hyphal cells which are densely filled with coarse granular cytoplasm.

In *Pucciniastrum abieti-chamaenerii* the nuclei undergo division and a septum is laid down in a plane that is parallel to the leaf surface, so that the primordial cell is divided into two cells, which are at right angles to the epidermis. In Fig. 32 four cells are shown, the upper two of which have just divided. This material was poorly stained and it was difficult to make out the nuclei in all the cells. After division the cell adjacent to the epidermis expands greatly, while the lower cell apparently degenerates, since in the next stage these cells are practically empty. Division of the primordial cells takes place more or less simultaneously, and a compact group of cells is developed,

the upper ones expanding vertically so that their length becomes almost double their width. They are binucleate, filled with contents, and furnish a striking contrast to the empty cells below (Fig. 33). As growth continues the upper cells may divide again in the same plane, cutting off below a second cell. Such a case is shown in the lower two cells of Fig. 33, where two empty cells are shown below each of the upper ones. There is often a third division, and another septum is laid down in the same plane, resulting in three basal cells in a row. In every case the contents degenerates so that the cells appear to be empty. Thus we have a series of cells which have arisen by repeated division of the primordial cells, and these divisions, being in the same plane, have resulted in a row of cells. Since the contents of all cells except the terminal one degenerate, this upper cell is thus the potential teliospore. Earlier in this paper the term "teliospore initial" has been used to indicate the cell which gives rise directly to the teliospore. Since this terminal cell becomes the teliospore it may be referred to as the teliospore initial.

The initial may give rise to a teliospore without further division, or it may divide once to give a two-celled spore, or twice to give a four-celled spore. The division of the teliospore initial takes place in a different plane from that of the primordial cell. The axes of the spindles instead of being at right angles to the leaf surface are parallel to it, and the septum that is laid down is a vertical one. In Fig. 34 nine teliospore initials are shown, each with a row of two or three empty cells below. In five of these initials vertical septations have been laid down, and the walls of each cell have become slightly thickened.

Pucciniastrum epilobii differs from *P. abieti-chamaenerii* in the absence of a row of empty cells below the teliospore. The primordial cell usually divides only once, the upper cell becoming the teliospore initial. The lower cell is prominent in the early stages but later the contents begins to disappear, although the two nuclei may usually be found. The teliospore initial divides, laying down vertical septations, as in *P. abieti-chamaenerii*, and the mature spores are one- to four-celled. Two nuclei are present in each cell of the teliospore. As the spores mature the nuclei come together and fuse. Various stages in this process of fusion are shown in Fig. 35. At first the two nuclei are small and homogeneous, but as they move together the chromatin is heavily staining and each nucleus has an irregular outline. The fusion nucleus is often to be observed in a spireme stage, and two cells have been drawn illustrating this. In many of the spores there is a large nucleus which appears to be in a resting condition. Whether this precedes spireme formation, as in *Hyalopsora*, is not known, but it is probable that since the teliospores do not germinate immediately, the nuclei overwinter in a resting condition.

The teliospores of *Pucciniastrum abieti-chamaenerii* develop a thickened light brown wall, which may be 3 μ in thickness, according to Grove (10). In the upper part of each cell there is a thinner spot, the germ pore, which shows very clearly from a surface view. In Fig. 36 a group of mature teliospores has been drawn, each cell showing a germ pore in the upper wall. This

group comprises a few cells of the margin of a large extended crust of spores. The outermost cells are at the left-hand side of the drawing, and tend to be more rounded or regular than those in the centre of the group, which are very compact. This difference has also been noted by Grove (10) in his description of the mature spores . . . . "those in the middle of the sorus *Melampsora*-like, but at the periphery roundish or oval, and composed of 1-3 cells, *i.e.*, divided by longitudinal walls." The teliospores do not always occur in such extended crusts, but may be found in small isolated groups, or even singly. In the latter case the spores are regularly four celled, not three celled, as Grove has described.

5. *Uredinopsis*

Uredinopsis is the third genus of fern rusts that belong to the Pucciniastreae, and is probably the best known. Faull (5), in his study of the morphology, biology and phylogeny of these genera, reviewed the situation in *Uredinopsis* and considered that this is the most primitive genus. Bell (3) has pointed out a misconception in the distribution of the teliospores. Earlier workers had described them as being distributed throughout the mesophyll, but Bell found that they were situated just below the epidermis, particularly the lower epidermis, where they formed a layer. Little is known, however, of the manner in which the teliospores are formed, and if this rust is to be considered as primitive then such a developmental study might be expected to throw some light upon this question.

Five species have been found in the Temagami Forest Reserve, namely *U. osmundae* on *Osmunda claytoniana*, *O. regalis* and *O. cinnamomea; U. struthiopteridis* on *Pteretis nodulosa; U. atkinsonii* on *Asplenium filix-femina; U. phegopteridis* on *Thelypteris dryopteris*, and *U. mirabilis* on *Onoclea sensibilis*. The teliospores of all five species were collected in abundance during August and September, and material showing various stages in development was obtained. In the species that have been studied it has been found that there is a great similarity in the method of teliospore development. *Uredinopsis phegopteridis* has been selected and a detailed description will be given of this species. A few figures of *U. struthiopteridis* have also been included for the sake of comparison.

In *Uredinopsis phegopteridis* the infection is bounded by the vascular bundles of the leaf, and thus the area of a lesion is that of a leaf islet. Sections through these areas reveal occasional uredinia with numerous white spores. The character of the uredospores readily distinguishes this species from infections of *Hyalopsora*, which are very similar, but which have orange-colored uredospores. The structure of the leaf of *Thelypteris* is very simple, there being no palisade layer, while the mesophyll cells are large in size with abundant intercellular spaces. In the infected areas the mycelium is most abundant in the intercellular spaces just below the epidermis, and the first indication of teliospore formation is found in this region. The tip of a hyphal strand comes to lie immediately below the epidermal cell, and applied closely to it. A septum is laid down, cutting off the tip, which contains two nuclei

and considerable cytoplasm. These terminal cells are enlarged, in the majority of cases tending to be somewhat club-shaped, and these are the primordial cells. In Fig. 37 a single primordial cell is shown, immediately beneath the upper epidermis. The primordial cells are usually fewer below the upper epidermis, being found most abundantly beneath the lower epidermis, although they are occasionally to be found in the mesophyll. In *U. struthiopteridis* the primordial cells are similar, being formed by the enlargement of the terminal cell of a hyphal strand. Fig. 38 illustrates a primordial cell of *U. struthiopteridis* beneath one of the cells of the lower epidermis. This is a later stage than in Fig. 37, and indicates the beginning of the rounding up of the primordial cell, which is the next stage in development. These rounded cells are found in abundance in a heavy infection, and are readily recognized by their dense contents and definite outline.

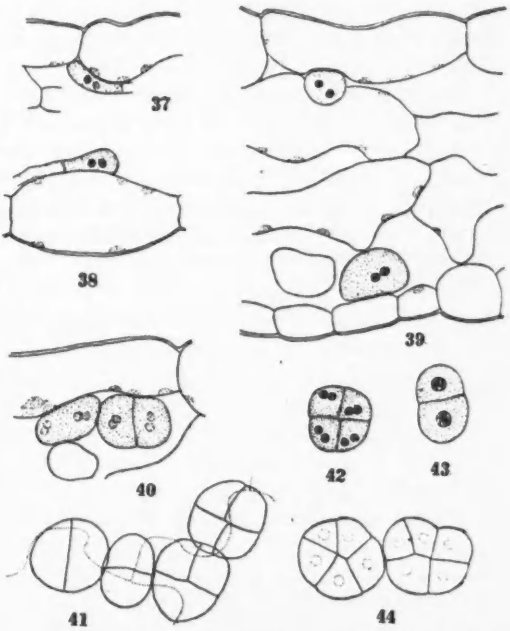

FIG. 37–44. *Uredinopsis. All figures* × *600.* FIG. 37. *Primordial cell of U. phegopteridis beneath the upper epidermis.* FIG. 38. *Primordial cell of U. struthiopteridis beneath the lower epidermis.* FIGS. 39–43. *U. phegopteridis.* FIG. 39. *A section through a frond showing two teliospore initials.* FIG. 40. *Division of the teliospore initial.* FIG. 41. *A group of young teliospores in the intercellular spaces below the epidermal cell walls, represented by dotted lines.* FIG. 42. *A typical four-celled teliospore.* FIG. 43. *A two-celled spore, each cell with a fusion nucleus.* FIG. 44. *Two multicellular teliospores of U. struthiopteridis.*

The rounded cells are potentially teliospores and since they have each arisen directly from a primordial cell they may be properly termed teliospore initials. The initial undergoes rapid growth, increasing greatly in size, and remaining close to the overlying wall. The appearance of this stage is well illustrated in the two initials that have been drawn in Fig. 39. The upper initial, which lies below the upper epidermis, is small and rounded, while beneath the lower epidermis is a somewhat larger initial in a later stage. The loosely arranged character of the mesophyll cells of the host is also shown in this figure. When the initials reach a certain size the nuclei undergo division and the two pairs of daughter nuclei move to the opposite ends (Fig. 40). After division has been completed a cross wall runs in and

the initial becomes two celled (Fig. 40). This cell is more properly termed a young teliospore, since it may mature without further division, thus giving rise to a two-celled teliospore. More often, however, the nuclei divide a second time and the teliospore may become either three celled or four celled. The mature spores of *U. phegopteridis* have never been found to contain more than four cells. Four typical teliospores are drawn in Fig. 41, and it will be noted that of these four, two are two celled, one is three celled, and the remaining one is four celled.

The intercellular spaces lying below the lateral walls of the epidermal cells are favorite places for teliospore formation in *U. phegopteridis*. The primordial cell in Fig. 37 is developing in just such an intercellular space. The four spores that are drawn in Fig. 41 are also lying below the side walls of the epidermal cells, the walls being represented as dotted lines. This group is part of a larger group, and if the drawing were extended in either direction it would be found that the majority of the spores would lie beneath the lateral walls. In a prepared section, two nuclei are found in each cell of the mature teliospore (Fig. 42). Although fusion has not been observed a large fusion nucleus is later formed. There is some indication that the nuclei of the teliospore in Fig. 43 have just fused, but in most cases the nuclear details are difficult to observe. In material that has been collected late in the growing season each cell contains a single nucleus, which appears to be in a resting condition. The mature teliospores of *U. struthiopteridis* are multicellular, and very irregular, each cell containing a single fusion nucleus (Fig. 44). The teliospores of *U. osmundae* are similar in every way to those of *U. struthiopteridis*. They are large, many celled and display a wide variation in shape, size and number of cells. This species furnishes an excellent example of the so-called polar furrowing in the arrangement of the septations of the mature teliospores.

Discussion

From a phylogenetic standpoint the Pucciniastreae have been regarded as primitive rusts and the fern rusts as the most primitive genera. Since the rusts show a high degree of specialization and have presumably evolved along with their hosts, we would expect to find the more primitive rusts upon those hosts which have evolved the least, namely the Pteridophytes. Arthur (1) considered the fern rusts to be primitive and based his argument upon the assumption that "the rusts on the most ancient line of hosts would be likely to reveal more primitive features than those on hosts of later origin." Upon the oldest family of rust-bearing ferns, the Osmundaceae, there was a species of *Uredinopsis*, parasitic on *Osmunda*, which Arthur considered to be the most primitive genus. The genera *Hyalopsora* and *Milesia* were found on various hosts of the Polypodiaceae and were considered to show an advance over *Uredinopsis*. Faull (5) has discussed the Pucciniastreae from a phylogenetic standpoint and has placed *Uredinopsis* as the most primitive rust, with *Milesia* closely related. The evidence upon which these assumptions are made is based primarily upon a study of the morphological features of the spore forms of the various genera concerned.

Despite the fact that in the Pucciniastreae there is a wide variation in the type of teliospore formed, it is significant that in the stages of development of both the intra-epidermal and subepidermal forms there is a general situation that appears to be common to all. The mycelium cuts off certain hyphal cells, which by growth and enlargement become the primordial cells. The primordial cell gives rise to a teliospore initial, which is intercellular in the species possessing subepidermal teliospores, and intracellular in those species which have the teliospore inside the epidermal cells. In the former the initials arise either directly by the rounding up of the primordial cell or after a number of divisions, while in the latter the initial is formed by the penetration of the wall of the epidermal cell, and the passage of the contents into the interior. By growth and division the initial gives rise to a multicellular teliospore, which may be thin walled or thick walled and which may germinate with or without a period of rest. The mature teliospores may be solitary or in groups, forming small to extended crusts; if in the epidermal cell, they may be scattered or in groups completely filling the cell. In all the species that have been studied, the teliospore is the product of a single primordial cell, whether it be many celled or few celled.

In the formation of primordial cells there is some variation in the species that have been studied. In *Calyptospora goeppertiana* the epidermis is separated from the cortex by the large number of primordial cells produced. A surface view indicates that the epidermal cells may be fairly completely "covered" by the large irregular closely packed primordial cells. In *Milesia*, however, the number of cells is greatly reduced and they occur in small groups or more often singly. They are also much larger than those of *Calyptospora*. There are two kinds of primordial cells in *Thecopsora vacciniorum*. The first are large and very irregular, and are found beneath the lower epidermis where the intercellular spaces are large. The other type of cell is narrow and elongated and is formed below the upper epidermis where the primordial hyphae force their way toward the epidermis through the compact palisade layer. They are accordingly at right angles to the leaf surface with the upper end flattened against the lower wall. The primordial cells of the two species of *Pucciniastrum* on *Epilobium* are subepidermal, small and somewhat flattened in cross section. In *P. epilobii* they form loosely arranged groups of varying size, while in *P. abieti-chamaenerii* they are more abundant forming large extended crusts, which appear to arise from a hyphal complex. The genus *Uredinopsis* possesses a comparatively simple type of primordial cell development. The tip of a hyphal strand growing below the epidermis becomes cut off and this cell enlarges somewhat to become the primordial cell. These club-shaped cells are characteristic of all the species of *Uredinopsis* that have been studied.

The teliospore initial in the intra-epidermal species arises directly from the primordial cell by the penetration of the host wall, and the passage of the contents through the wall to form a rounded or sac-like body. The initial appears to become independent since it now possesses the entire cell

contents and in its further development loses all connection with the primordial cell. In *Calyptospora* the initials are small and rounded with many in a single cell. In *Milesia* they are similar to those of *Calyptospora*, except that they are formed in the epidermis of the leaves, and are fewer in number. *Thecopsora* resembles *Milesia* very closely, though the initial is somewhat sac-like with a narrowed base. In the subepidermal species, as in *Pucciniastrum*, they arise by division of the primordial cells, which cut off a row of vertical cells, the terminal ones becoming the initials while the lower ones lose their contents. These empty basal cells are most striking in *P. abietichamaenerii* and form a decided contrast to the compact group of initials just above them. The formation of teliospore initials in *Uredinopsis* takes place simply by the rounding up of the primordial cells.

The penetration of the host cell wall by the primordial cell and the haustorial mother cell might be briefly compared. *Calyptospora* is very suitable for such a study since early stages in the development of the initials were found in abundance. The primordial cell and the haustorial mother cell are similar in many ways although the former is much larger and its function is considerably different. According to Rice (19), in haustorial formation the wall becomes pierced and a small but definite papilla appears projecting slightly beyond the inner wall. The haustorium proper is formed at the end of this papilla. Moss (16) has some 30 figures of haustoria of the Pucciniastreae and this beak-like part, which extends through the cell wall, is a characteristic feature. In the penetration by the primordial cell there is a definite opening in the wall but papillae have not been found. In *Calyptospora*, as soon as the wall is pierced, the contents forms a small rounded sac-like body, the teliospore initial, which reveals no suggestion of a rod-like penetration tube. In the material studied by the writer there was never any difficulty in distinguishing the young initials from haustoria. Penetration of the cell wall undoubtedly takes place in the same manner as in the formation of haustoria. In their function and further development, however, the teliospore initials are radically different from haustoria.

On the basis of development, the species that have been studied fall readily into three general groups or types. In the first group the method of development is very simple. The primordial cells round up to form the teliospore initials, which lay down septations to form the teliospores directly. This is well illustrated by the developmental situation as found in *Uredinopsis*. The point of interest here is that *Uredinopsis* is generally considered to be the most primitive rust, and it also possesses a simple type of teliospore development. If a simple type of development may be regarded as a primitive character, then it is quite possible that *Uredinopsis* is the most primitive genus in the Pucciniastreae.

The second method of development is one where the primordial cells occupy the same relative position, but instead of becoming initials directly the host wall above becomes pierced, and the initials are formed *inside* the epidermal cell. The contents passes in and the initial enlarges to form the

intra-epidermal teliospore. This type of development is found in four genera, *Calyptospora*, *Milesia*, *Hyalopsora* and *Thecopsora*. In *Calyptospora goeppertiana* the teliospores are formed in the epidermal cells of the stems during the summer and completely fill every cell with thick-walled resting spores. *Hyalopsora aspidiotus* differs in that the spores are formed in the young fronds in the spring, and are thin walled and germinate immediately. In *Milesia marginalis*, *M. polypodophila* and *M. intermedia* the spores are similar to *H. aspidiotus*, but differ in that they are formed in the overwintered fronds in the spring. *Milesia fructuosa*, however, develops teliospores at the end of the growing season. *Thecopsora vacciniorum* differs from *M. fructuosa* only in that the teliospores overwinter and germinate in the spring.

In the third type the primordial cells tend to be aggregated in groups, and by division form a crust of initials which lay down anticlinal walls to form teliospores. This method of development is found in the genus *Pucciniastrum*. In *P. epilobii* the primordial cell usually divides once to give an empty basal cell, and an upper cell, which is the teliospore initial. This may be carried still further in *P. abieti-chamaenerii* where the primordial cell undergoes a number of divisions, cutting off a row of empty basal cells. The initial is greatly elongated, and as vertical septations are laid down the walls become greatly thickened. The teliospores thus become closely packed in groups, and may cover a considerable area.

These three general types seem to indicate two lines of development. With *Uredinopsis* as a starting point we have a subepidermal primordial cell which rounds up to form a teliospore initial, giving rise to a multicellular teliospore. Were the teliospore initial to be formed *inside* the epidermal cell instead of below, we would have the situation as now understood in *Milesia*, *Calyptospora*, *Thecopsora* and *Hyalopsora*. Thus, there seems to be a line of development culminating in the genera with intra-epidermal teliospores. The other line of development also begins with *Uredinopsis*, but leads through *Pucciniastrum* giving a compact subepidermal group. This is accomplished by the increase in number of the primordial cells and therefore in the number of teliospore initials. This line has tended more towards the sorus type of teliospore group. In *Melampsoridium betulinum* the teliospores are single celled and form small compact clusters, which arise from primordial cells, as in *Pucciniastrum*. In *Melampsora* there is said to be a definite sorus. The writer has studied early stages of *M. medusae* in a preliminary way and has found a group of primordial cells developing below the epidermis, as in *Pucciniastrum*, and in its manner of development it is similar to that of *Melampsoridium*. Hence, this series from *Uredinopsis* may lead through *Pucciniastrum* and *Melampsoridium* to *Melampsora*.

These results agree in a very general way with the phylogenetic tree that Faull (5) has constructed for the *Pucciniastreae*, except for the possibility that the two lines of development indicated above might represent two phylogenetic series. In that case, the phylogenetic tree would possess two main branches, both beginning at *Uredinopsis*, the one leading through the

intra-epidermal forms, *Milesia*, *Hyalopsora*, *Thecopsora* and *Calyptospora*, and the other passing through the subepidermal genera *Pucciniastrum* and *Melampsoridium*, to such forms as *Melampsora*. Many more data would be necessary, however, before this series could be postulated as a phylogenetic one.

These primitive rusts possess certain characters which they share with members of the Auriculariales and which point to their close relationship. Many authors have called attention to the fact that certain of the Auriculariales were rust-like and the similarity of the basidium and the promycelium has been often emphasized. It is quite generally conceded also that the probasidium and the teliospore are homologous structures (Gäumann (9), Linder (15)). It may be shown, moreover, that from the standpoint of their development there is a striking similarity. In *Uredinopsis* the teliospore has its origin in a terminal hyphal cell which has been called the primordial cell. The probasidium in *Iola*, *Saccoblastia* and in certain species of *Septobasidium* has its origin also in a hyphal cell, usually terminal in position, which is homologous with the primordial cell of *Uredinopsis*. It is significant also that in those forms in which the probasidium is not greatly differentiated, as in some species of *Septobasidium* and *Platygloea*, and also in such genera as *Eocronartium*, where the probasidium is entirely lacking, the origin of the basidium is in a hyphal tip, as in *Uredinopsis*.

The nuclear situation in the hyphal tip which gives rise to the probasidium in the Auriculariales is like that of the developing teliospore of the fern rusts. Two nuclei are always present and these come together and fuse as the probasidium matures. In *Iola*, Gäumann (8) found that as soon as the nuclei fused in the mature probasidium, germination took place and the fusion nucleus passed through all stages of prophase before entering into the basidium. A similar situation has been found in *Milesia* and *Hyalopsora* where the two nuclei fuse and immediately enter into heterotypic prophase before passing out into the promycelium. While very few of the Auriculariales have been studied cytologically it is interesting to note here that in *Eocronartium*, which has been described by Fitzpatrick (7), the details of nuclear fusion and meiotic prophase are practically identical with those of *Hyalopsora*. The fact that heterotypic prophase occurs in the teliospore and probasidium would lend support to the idea that the promycelium is an interpolated structure, since in the primitive condition not only prophase but anaphase and telophase took place in the spore itself.

This evidence is in line with the suggestion of Linder (15) that the Auriculariales have been derived from the Uredinales and not the reverse, as Neuhoff (17) and Gäumann (9) believed. It is suggested here that the Auriculariales have arisen from some point on the basic rust line near *Uredinopsis*, *Milesia* and *Hyalopsora*, through such genera as *Iola* with a well-defined probasidium, *Septobasidium* which displays a gradual reduction in the probasidium, *Platygloea* where it has practically disappeared, to such forms as *Eocronartium* and *Auricularia*.

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A COMPARISON OF VARIOUS HARVESTING METHODS IN RESPECT TO MOISTURE AND GRADE OF THE GRAIN[1]

(INTERIM REPORT)

BY R. K. LARMOUR[2], W. F. GEDDES[3] AND D. CAMERON[4]

Abstract

In a moisture and grade survey of grain harvested by various methods in western Canada during the 1932-1933 season it was found that straight-combined wheat showed a greater percentage of tough and damp samples than either stook-threshed or swath-combined samples. Of 401 stook-threshed samples 3% were tough or damp; of 416 straight-combined samples 22% were tough and 3% damp; and of 211 swath-combined samples 8% were tough and 1% damp.

With respect to grade, it was found that as a result of exposure to rains the average grade lowering was least for stooked grain and greatest for swath-combined grain.

Since the introduction of the combine-harvester into western Canada, statements have been made occasionally to the effect that combine-threshed wheat, especially that harvested by the straight-combine, is more liable to damage by heating than grain threshed from the stook. This has been attributed to (1) the tendency of operators to cut the grain containing too much moisture; (2) the presence of green weed seeds; (3) the presence of green kernels in grain from fields that have matured unevenly; (4) the failure of the grain to undergo the so-called "sweating-process" before it goes to the bin.

It seems likely that in some cases the farmer may begin combining too soon. The temptation to do so is great because the standing grain is subject to damage by wind, rain, hail and snow. Furthermore wheat will handle nicely in the combine several days before it gets below 14.4% moisture. The mistake of starting too soon, although made in the early days of use of this machine, is not now as common with experienced operators. Probably this factor will always have to be watched closely by buyers.

The presence of green kernels owing to uneven ripening is a matter for serious concern in some seasons, and in rolling country will always be a difficulty in the way of successful combining. The machine operator, faced with the alternative of going around or through a low spot containing a little immature grain, will usually take the latter course, hoping that there will be enough dry grain and that there will be sufficient mixing to reduce the moisture content of the bulk to a safe level.

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Green weed seeds, particularly those of Russian thistle, are extremely difficult to separate in a small thresher. In dry seasons, such as 1931-1932, when this weed was particularly prevalent, much of the wheat was heavily contaminated. Many weeds are not nearly ripe at time of harvesting, and consequently the seeds and parts of the stems break off and go into the wheat. The moisture content of such seeds may run as high as 60% and on account of their softness they tend to stick together in masses, which create centres of heating. This trouble is avoided in stook-threshing because the weeds, after cutting, desiccate fairly rapidly in normal weather, and the dry seeds even though they get into the grain are not a source of danger.

The sweating process is probably due to colloidal changes. It appears that the moisture which apparently increases in the outer layers of the kernels does not represent a loss or gain for the whole bulk, but is merely a matter of changed distribution. If this is the correct explanation there appears to be no reason why wheat should not undergo the change in the head as well as in the stook, but the general opinion of farmers and buyers is that this is not the case. It is thought that unless wheat sweats in the stook, it will sweat in the bin, and in the latter event will heat as a result of the moisture apparently produced in the process. Some grain men think that the difficulty of judging moisture of straight-combined grain is due to the fact that it has not sweated. Cases have been reported of grain reputed to be sound and dry going out of condition in transit.

These questions cannot be settled satisfactorily in the laboratory, and therefore it was decided that a survey of harvesting methods should be carried out in order to ascertain to what extent the various statements and beliefs previously mentioned, are warranted. To this end, during the harvest season

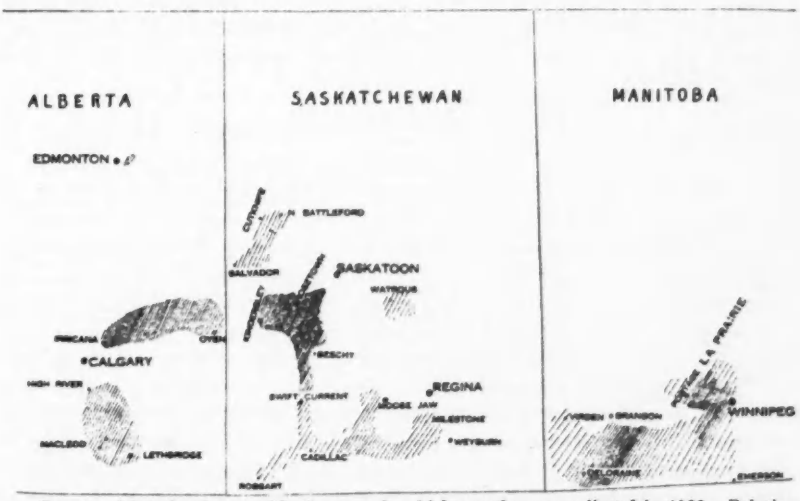

FIG. 1. *Map showing roughly the areas in which samples were collected in 1932. Relative numbers indicated by intensity of shading.*

of 1932, samples from machines in operation and from loads and bins of grain were collected by men sent out by the Universities of Manitoba, Saskatchewan and Alberta. The samples were taken in air-tight tins which were shipped each day to the respective laboratories where they were submitted to moisture determinations. Operations were confined to those areas in which a fairly large number of combines or swath-combines were operating. The districts covered in the three provinces are shown approximately by the map in Fig. 1.

The collections can be roughly divided into three parts: (1) the early harvest season, during which the weather was dry in all provinces and a large number of samples were collected under conditions in which the results were largely a reflection of farmers' judgments as to the proper time to begin operations; these data are especially valuable in connection with straight combining; (2) a short period during which harvesting operations were resumed for about two to three days following a fairly heavy rain; and (3) the remainder of the harvest season, after two or more rains had occurred. The numbers of samples collected in these periods in each of the provinces are given in Table I.

TABLE I

CLASSIFICATION OF SAMPLES ACCORDING TO METHOD OF HARVESTING, EXPOSURE TO RAINFALL AND ORIGIN

	Before rain		After one rain		After two or more rains		Grand total	
	No.	%	No.	%	No.	%	No.	%
Stook-threshed								
Manitoba	136	13.2	13	1.3	61	5.9	210	20.4
Saskatchewan	65	6.3	8	0.7	62	6.1	135	13.1
Alberta	3	0.3	2	0.2	51	5.0	56	5.5
Total	204	19.8	23	2.2	174	17.0	401	39.0
Straight-combined								
Manitoba	39	3.8	13	1.3	19	1.8	71	6.9
Saskatchewan	57	5.5	13	1.3	175	17.0	245	23.8
Alberta	26	2.5	21	2.0	53	5.2	100	9.7
Total	122	11.8	47	4.6	247	24.0	416	40.4
Swath-combined								
Manitoba	103	10.0	4	0.4	44	4.3	151	14.7
Saskatchewan	9	1.0	2	0.2	23	2.2	34	3.3
Alberta	0	0	2	0.2	24	2.3	26	2.6
Total	112	11.0	8	0.8	91	8.8	211	20.6
Grand totals								
All methods	438	42.6	78	7.6	512	49.8	1028	

The total number of samples collected was 1,028; of these 39% were stook-threshed, 40% straight-combined, and 21% swath-combined; with respect to weather, 42.5% were collected before any rain, 7.5% after one rain, and 50% after two or more rains.

In a study like this, the two important considerations are the moisture content and the grade. For the sake of simplicity in the tabulations, we shall deal with these separately. In summarizing the moisture data, the durum wheat samples have been included with the common, because with respect to moisture the class of wheat should exercise no marked effect.

Moisture in Wheat Samples Harvested before Rain

A summary of the distribution of moisture in this class is given in Table II. In this group there should appear evidences of the total effect of (a) the tendency to start combining too early, (b) unevenness in ripening, (c) green weed seeds if present to any appreciable extent. With both stook-threshed and swath-combined methods the samples showing moisture contents below 14.5% represented 98% of their respective totals, while with the straight-combined method, 12% were tough and 4% damp. The number in each group is sufficiently large to make this difference fairly significant, and it must be concluded therefore that in the early part of the harvest season, the tendency for straight-combined wheat to be tough or damp is appreciably greater than for stook-threshed or swath-combined grain. It should be noted too that the average moisture content of the straight-grade samples was higher for the straight-combined wheat than for the others. From the stook and swath there were 32 and 45% of the samples respectively that showed moisture below 10.9%, while only 3% of the straight combined were below this value. In fact, in the 416 samples of straight-combined grain, only 19 or 4.6% had a lower moisture content. This of course is a consequence of the fact that when standing grain gets to this moisture level it is too ripe, and is subject to heavy loss by shelling, and farmers therefore try to harvest just as soon as possible after the grain dries to below 14.4% or what they judge to be "straight-grade" moisture.

Samples Harvested after One Rain

This group, though small, comprising only 77 samples or 7.5% of the whole series, is very interesting because the rain was heavy enough to stop all harvesting operations in the districts in which the writers were interested. It was followed by good drying weather which lasted just long enough to permit a partial resumption of operations. While it is obviously impossible in a summary such as this to examine the circumstances of each particular case, it would appear probable that this group includes samples from the more impatient operators and from those having the poorer judgment regarding the fitness of wheat for threshing. Examination of Table III shows that only three out of 23, or 13% of the stook samples, were tough; 14 out of 46, or 30% of the straight-combined samples, were tough, and 2% of them were damp, while six of the eight swath samples were tough. These data may be interpreted as evidence either that the combine operators were too anxious to begin or that their judgment was poor.

TABLE II

DISTRIBUTION OF MOISTURE IN SAMPLES COLLECTED EARLY IN THE HARVEST SEASON, BEFORE ANY RAIN HAD OCCURRED. COMMON AND DURUM WHEAT

Moisture range %	Stook-threshed						Straight-combined						Swath-combined					
	Man.	Sask.	Alta.	Total	%	Av. moisture	Man.	Sask.	Alta.	Total	%	Av. moisture	Man.	Sask.	Alta.	Total	%	Av. moisture
Straight grade																		
< 10.9	54	10	1	65	32	10.2	—	2	2	4	3	10.4	50	2	—	52	46	10.3
10.9–11.7	41	14	1	56	27.5	11.2	14	8	5	27	22	11.4	31	2	—	33	30	11.3
11.8–12.6	26	18	1	45	22	12.2	8	16	6	30	25	12.2	10	3	—	13	12	12.2
12.7–13.5	6	17	—	23	11	13.0	5	15	6	26	21	13.0	6	1	—	7	6	13.1
13.6–14.4	7	5	—	12	6	14.0	6	5	5	16	13	14.0	4	1	—	5	4	13.9
Tough																		
14.5–15.3	—	1	—	1	0.5	14.6	3	6	1	10	8	14.9	1	—	—	1	1	14.9
15.4–16.2	1	—	—	1	0.5	16.2	1	2	—	3	3	15.6	—	—	—	—	—	—
16.3–17.0	1	—	—	1	0.5	16.6	—	—	1	1	0.8	17.0	—	—	—	—	—	—
Damp																		
17.1–17.9	—	—	—	—	—	—	1	1	—	2	1.7	17.5	—	—	—	—	—	—
18.0–18.8	—	—	—	—	—	—	—	1	—	1	0.8	18.4	—	—	—	—	—	—
18.9–19.7	—	—	—	—	—	—	1	1	—	2	1.7	20.9	1	—	—	1	1	19.4
Total in each group				204						122						112		
Total in series				438														

TABLE III

DISTRIBUTION OF MOISTURE IN WHEAT SAMPLES CUT AFTER ONE RAIN

Moisture range %	Stook-threshed						Straight-combined						Swath-combined					
	Man.	Sask.	Alta.	Total	%	Av. moisture	Man.	Sask.	Alta.	Total	%	Av. moisture	Man.	Sask.	Alta.	Total	%	Av. moisture
Straight																		
< 10.9	—	—	1	1	4	10.2	—	—	3	3	6	10.5	—	—	—	—	—	—
10.9–11.7	—	—	1	1	4	11.3	—	—	3	3	6	11.3	1	—	—	1	12.5	11.2
11.8–12.6	4	—	—	4	18	12.4	1	1	5	7	15	12.2	—	—	—	—	—	—
12.7–13.5	6	2	—	8	35	13.1	2	1	3	6	13	13.1	—	—	1	1	12.5	13.2
13.6–14.4	3	3	—	6	26	14.1	5	5	2	12	26	14.0	—	—	—	—	—	—
Tough																		
14.5–15.3	—	—	—	—	—	—	5	2	—	7	15	14.9	2	1	1	4	50	15.0
15.4–16.2	—	2	—	2	9	15.9	—	1	—	1	2	15.7	1	1	—	2	25	15.6
16.3–17.0	—	1	—	1	4	16.5	—	2	4	6	13	16.6	—	—	—	—	—	—
Damp																		
17.1–17.9	—	—	—	—	—	—	—	—	1	1	2	17.4	—	—	—	—	—	—
18.0–18.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
18.9–19.7	—	—	—	—	—	—	—	1	—	1	2	19.2	—	—	—	—	—	—
> 19.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total in each group				23						47						8		
Total series, 78 samples																		

Samples Collected after Two or More Rains

Table IV shows a summary of the samples collected after the second and subsequent rains. It should be observed here that this occurrence of two heavy rains in rather close succession had the effect of postponing harvesting operations in the combine area of Saskatchewan and Alberta for two to three weeks after the grain had become fit for harvesting. The most important consequence of this was that one of the reputed sources of trouble, namely, unevenness of ripening, was almost wholly removed because, during the period required for the standing grain to become dry enough to cut, the slower maturing heads had a chance to ripen. This partly accounts for the evenness and high grade of the combined samples of this season.

Furthermore, owing to better climatic conditions in the growing period, wheat had a vigorous growth and the Russian thistle was less prevalent than in the previous year. Other weeds ripened during the two to three week delay previously mentioned and hence combined wheat was in nearly all cases almost free from green weed seeds. The incidence of tough and damp samples shown in Table IV therefore must be attributed largely to the too early resumption of operations and again, this was due to anxiety, poor judgment, or both.

In this group there were 247 straight-combined samples, of which 3% were damp, 25% tough and 72% straight grade; 174 stook-threshed samples of which 3% were tough and 97% straight; and 91 swath samples of which 2% were damp, 9% tough and 89% straight grade. Most of the straight-combined samples in this group were collected in Saskatchewan. After the rains of August 29 to 31, the weather conditions were quite favorable for harvesting. There were only slight local showers from then until the end of the collection period. It must be concluded therefore that there may be, even under the most favorable conditions, a relatively high percentage of straight-combined wheat cut in the tough stage.

Part of the trouble, particularly in the latter part of the harvest season, seemed to be due to the fact that the straw, having become practically dead, dries out fairly rapidly when standing, and the farmer, accustomed to judging the fitness of grain by the condition of the straw, starts his machine when the straw is brittle enough to thresh properly. This criterion is generally satisfactory for stooked grain because the heads, being more open and exposed, dry more rapidly after a heavy rain than the more closely packed straw, and thus, when the straw is fit for threshing, the grain usually is also fit. This does not hold in the case of standing grain. The writers were able to procure a small series of samples under conditions that show this very clearly.

On September 9 about midnight, the weather in the Rosetown area suddenly changed from hot and dry to cool and cloudy, and a very slight amount of rain, too small to be recorded except as a trace, fell. This was followed by a very heavy mist which lasted until about 7 a.m. September 10. The weather remained cool and cloudy until 10 a.m. when it cleared and became warmer. Stook threshing was resumed at about 3 p.m., but the combines

TABLE IV

DISTRIBUTION OF MOISTURE IN SAMPLES COLLECTED AFTER TWO OR MORE RAINS

Moisture range %	Stook-threshed						Straight-combined						Swath-combined					
	Man.	Sask.	Alta.	Total	%	Av. moisture	Man.	Sask.	Alta.	Total	%	Av. moisture	Man.	Sask.	Alta.	Total	%	Av. moisture
Straight																		
< 10.9	5	3	15	23	13	10.2	—	6	6	12	5	10.6	6	—	3	9	10	10.4
10.9–11.7	15	16	13	44	25	11.4	5	26	8	39	16	11.3	3	1	5	9	10	11.4
11.8–12.6	15	21	12	48	28	12.3	2	24	15	41	17	12.1	9	7	10	26	29	12.3
12.7–13.5	17	14	7	38	22	13.1	1	28	8	37	15	13.0	16	6	5	27	30	13.1
13.6–14.4	7	5	3	15	9	13.9	6	37	5	48	19	14.0	6	3	—	9	10	14.0
Tough																		
14.5–15.3	—	3	1	4	2	14.8	1	29	5	35	14	14.9	3	1	1	5	5	14.9
15.4–16.2	2	—	—	2	1	15.2	3	16	2	21	8	15.8	—	2	—	2	2	15.8
16.3–17.0	—	—	—	—	—	—	—	5	3	8	3	16.5	—	2	—	2	2	16.7
Damp																		
17.1–17.9	—	—	—	—	—	—	—	1	1	2	1	17.4	1	—	—	1	1	17.1
18.0–18.8	—	—	—	—	—	—	1	3	—	4	2	18.3	—	1	—	1	1	18.5
18.9–19.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19.8–20.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
> 20.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total in each group				174						247						91		
Total in series				512														

stood idle until about 6 p.m. Samples of stook, combine and swath grain were collected in order to ascertain the effect of this particular weather condition. The results, given in Table V, show that of 17 stook samples only 6% were tough; of 27 combine samples 37% were tough and 7% damp; of 15 swath samples, 26% were tough and none damp. The strange thing

TABLE V

SAMPLES COLLECTED ON SEPTEMBER 10, 3 TO 9 P.M., AFTER A VERY SLIGHT SPRINKLE OF RAIN FOLLOWED BY MIST AND CLOUDY WEATHER

Moisture range %	Stook			Combine			Swath		
	No.	%	Average moisture	No.	%	Average moisture	No.	%	Average moisture
10.9–11.7	1	6	10.9	2	7.4	11.1	—	—	—
11.8–12.6	6	35	12.4	1	3.7	11.8	5	33.3	12.3
12.7–13.5	8	47	13.0	4	15.0	13.2	4	24.6	12.9
13.6–14.4	1	6	13.8	8	29.6	13.9	2	12.3	14.1
Tough									
14.5–15.3	1	6	14.6	6	22.2	14.9	1	6.7	14.8
15.4–16.2	—	—	—	2	7.4	15.8	1	6.7	15.9
16.3–17.0	—	—	—	2	7.4	16.5	2	12.3	16.7
Damp									
17.1–17.9	—	—	—	1	3.7	17.1	—	—	—
18.0–18.8	—	—	—	1	3.7	18.2	—	—	—
Totals	17			27			15		

about this was that the stooks appeared to be on the tough side, while the standing grain in all cases was brittle and in good threshing condition. In the case of the stooks, the inside of the sheaves was very dry and even though the outer heads were quite tough, they formed so small a percentage of the whole that the representative sample taken from the load was quite dry. The combine grain was uniformly higher in moisture and the lag of drying in the head, probably owing to protection by the glumes, resulted in a tough sample.

A general summary of all the moisture data is given in Table VI. This includes Tables II, III and IV, Table V having already been included in Table IV. Of the 401 stook-threshed samples only 3% were tough and none were damp; of the 416 straight-combined samples 22% were tough and 3% damp; and of 211 swathed samples, 8% were tough and 1% damp. It may be concluded from these data that there is a much greater tendency for straight-combined wheat to run tough or damp than grain harvested by other methods. The prevailing harvest weather, despite the rains that occurred in the earlier part, was on the whole, very favorable. If under such circumstances 25% of the samples were tough or damp, it might be expected that in an unfavorable season, the percentage would be larger.

TABLE VI

DISTRIBUTION OF MOISTURE, ALL WHEAT SAMPLES COLLECTED

Moisture range %	Stook-threshed						Straight-combined						Swath-combined					
	Man.	Sask.	Alta.	Total	%	Av. moisture	Man.	Sask.	Alta.	Total	%	Av. moisture	Man.	Sask.	Alta.	Total	%	Av. moisture
Straight grade																		
< 10.9	59	13	17	89	22.2	10.2	—	8	11	19	4.6	10.5	56	2	3	61	28.9	10.3
10.9–11.7	56	30	15	101	25.2	11.3	19	34	16	69	16.6	11.3	35	3	5	43	20.4	11.3
11.8–12.6	45	39	13	97	24.2	12.3	11	41	26	78	18.7	12.1	19	10	10	39	18.5	12.3
12.7–13.5	29	33	7	69	17.2	13.1	9	44	17	70	16.8	13.0	22	7	6	35	16.6	13.1
13.6–14.4	17	13	3	33	8.2	14.1	17	47	12	76	18.3	14.0	10	4	—	14	6.6	13.9
Totals				389	97.0					312	75.0					192	91.0	
Tough																		
14.5–15.3	—	4	1	5	1.2	14.7	9	37	6	52	12.5	14.9	6	2	2	10	4.6	14.9
15.4–16.2	3	2	—	5	1.2	15.6	4	19	2	25	6.0	15.8	1	3	—	4	1.9	15.7
16.3–17.0	1	1	—	2	0.5	16.5	—	7	8	15	3.5	16.6	—	2	—	2	1.0	16.7
Totals				12	3.0					92	22.0					16	7.5	
Damp																		
17.1–17.9	—	—	—	—	—	—	1	2	2	5	1.2	17.4	1	—	—	1	0.5	17.1
18.0–18.8	—	—	—	—	—	—	1	4	—	5	1.2	18.3	—	1	—	1	0.3	18.5
18.9–19.7	—	—	—	—	—	—	—	1	—	1	0.3	19.2	1	—	—	1	0.5	19.4
19.8–20.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
> 20.6	—	—	—	—	—	—	—	1	—	1	0.3	20.6	—	—	—	—	—	—
Totals										12	3.0					3	1.5	
Grand totals				401						416						211		

Total series, 1,028 samples

In concluding the discussion of moisture, it should be noted, as a matter of record, that of the 71 tough and damp samples in the Saskatchewan group, only one was graded into the local elevator as tough, that one being the sample with 20.6% moisture. In all other cases, the buyers took the grain in as straight grade, and as there was a great proportion of cash sales, loss could easily be avoided by mixing with drier grain of the same grade. The buyers in areas where a great deal of straight combining is done, professed to have no apprehension about handling it. In these districts the farmers are guided to a large extent by the judgment of the buyer; they take in a batch from the first round of the machine and get the buyer's opinion regarding its fitness. If the buyer thinks the grain a little too tough, he advises the operator to wait for a day or two, and usually this advice is acted upon. On the other hand, in districts where few combines are used, there is often a reciprocal distrust between farmer and buyer, the farmer suspecting unwarranted bias on the part of the buyer, who in turn is inclined to discount combined grain unduly because he has not handled enough to have learned the limits of safety. This attitude is somewhat justified, because generally the districts having few combines operating are those to which they have proved unsuitable owing to rolling topography, or late ripening period. Briefly then, the buyers who condemned most vigorously the straight combine were those who had the least of this kind of grain to handle. In the Saskatchewan survey there were encountered very few buyers who admitted having lost cars from heating.

The Relation of Harvesting Method to the Grade of the Sample

The season of 1932 was rather unsuitable for a study of grade because, owing to factors already discussed, the crop was very uniform, practically none of it grading below No. 3 Northern, and by far the largest percentage grading No. 1 Hard or No. 1 Northern. This narrows down the range and makes differentiation on this basis more difficult than if there had been a wider grading range.

Only the Manitoba and Alberta samples were officially graded, and the results from these provinces have been collected in Tables VII and VIII, the former showing the division according to weather and the latter showing a summary of the whole series. The durum samples have been treated separately in Table IX.

Considering Table VII, it can be seen that in the collections made before any rain, the percentage of samples in the four grades was nearly the same for both stook- and straight-combined samples, being 32–35% No. 1 Hard, 47% No. 1 Northern, 13–14% No. 2 Northern and 4% No. 3 Northern (the combined samples are quoted first). The swathed samples showed only the top three grades, No. 1 Hard and No. 1 Northern each representing 46.5% of the total number; there were thus more No. 1 Hard samples by this method than by either of the other two.

TABLE VII

DISTRIBUTION OF SAMPLES ACCORDING TO GRADE

Grade	Stook-threshed				Straight-combined				Swath-combined				Header barge	
	Man.	Alta.	Total	%	Man.	Alta.	Total	%	Man.	Alta.	Total	%	Alta.	%
Samples collected before rain														
1 Hard	32	1	33	35	7	8	15	32	20	—	20	46.5	1	12.5
1 Nor.	43	2	45	47	11	11	22	47	20	—	20	46.5	6	75
2 Nor.	13	—	13	14	1	5	6	13	3	—	3	7	1	12.5
3 Nor.	4	—	4	4	1	1	2	4	—	—	—	—	—	—
4 Nor.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 5	—	—	—	—	1	—	1	2	—	—	—	—	—	—
Sample grade	—	—	—	—	—	1	1	2	—	—	—	—	—	—
Total	92	3	95		21	26	47		43		43		8	
Average grade			0.87				0.96				0.60		1.00	
Samples collected after one rain														
1 Hard	1	1	2	40	1	5	6	26	1	—	1	50	—	—
1 Nor.	2	1	3	60	1	12	13	56	1	—	1	50	—	—
2 Nor.	—	—	—	—	—	2	2	9	—	—	—	—	—	—
Sample grade	—	—	—	—	—	2	2	9	—	—	—	—	—	—
Total	3	2	5		2	21	23		2		2			
Average grade			0.60				0.80				0.50			
Samples collected after two rains														
1 Hard	—	17	17	24	—	5	5	9	—	6	6	16	—	—
1 Nor.	11	24	35	49	—	19	19	34	2	11	13	35	—	—
2 Nor.	5	6	11	15	2	20	22	40	2	6	8	22	—	—
3 Nor.	2	3	5	7	—	6	6	11	—	1	1	3	—	—
4 Nor.	—	1	1	1	—	—	—	—	—	—	—	—	—	—
No. 5	—	—	—	—	—	1	1	2	—	—	—	—	—	—
2 Nor. rej.	3	—	3	4	—	—	—	—	2	—	2	5	—	—
3 Nor. rej.	—	—	—	—	—	—	—	—	1	—	1	3	—	—
4 Nor.	—	—	—	—	—	—	—	—	3	—	3	8	—	—
No. 5	—	—	—	—	—	—	—	—	3	—	3	8	—	—
Sample grade	—	—	—	—	—	2	2	4	—	—	—	—	—	—
Total	21	51	72		2	53	55		13	24	37			
Average grade			1.2				1.8				2.27			

TABLE VIII

SUMMARY SHOWING THE DISTRIBUTION OF GRADE FOR THE VARIOUS HARVESTING METHODS

Grade	Stook-threshed				Straight-combined				Swath-combined				Header barge	
	Man.	Alta.	Total	%	Man.	Alta.	Total	%	Man.	Alta.	Total	%	Alta.	%
1 Hard	33	19	52	30	8	18	26	21	21	7	27	33	1	12.5
1 Nor.	56	27	83	48	12	42	54	43	22	12	34	42	6	75
2 Nor.	18	6	24	14	3	29	32	26	5	6	11	13	1	12.5
3 Nor.	6	3	9	5	1	7	8	6	—	1	1	1	—	—
4 Nor.	—	1	1	1	—	—	—	—	—	—	—	—	—	—
No. 5	—	—	—	—	1	1	2	1.6	—	—	—	—	—	—
2 Nor. rej.	3	—	3	2	—	—	—	—	2	—	2	2	—	—
3 Nor. rej.	—	—	—	—	—	—	—	—	1	—	1	1	—	—
4 Nor. rej.	—	—	—	—	—	—	—	—	3	—	3	4	—	—
No. 5	—	—	—	—	—	—	—	—	3	—	3	4	—	—
Sample grade	—	—	—	—	—	3	3	2.4	—	—	—	—	—	—
Totals	116	56	172		25	100	125		56	26	82		8	
Average grade			1.04				1.35				1.40			

TABLE IX

SUMMARY SHOWING THE MOISTURE CONTENT FOR GRAIN HARVESTED BY THE VARIOUS METHODS

Method of harvesting	No. of samples collected	% of samples grading			Moisture			% of samples grading				Average grade
		Straight	Tough	Damp	Min. %	Max. %	Av. %	1 A.D.	2 A.D.	3 A.D.	4 A.D.	
Stook-threshed												
Before rain	44	100.0	—	—	10.5	13.9	11.6	97.7	2.3	—	—	1.02
After 1 rain	10	100.0	—	—	12.3	14.0	13.2	90.0	10.0	—	—	1.10
After 2 or more rains	40	97.5	2.5	—	10.6	15.3	12.7	60.0	37.5	—	2.5	1.55
								Mean for stook-threshed				1.25
Swathed and combined												
Before rain	60	96.7	1.7	1.7	10.3	14.0	11.5	98.3	1.7	—	—	1.01
After 1 rain	4	25.0	75.0	—	11.2	15.4	14.2	50.0	25.0	25.0	—	1.80
After 2 or more rains	31	87.1	9.7	3.2	10.6	14.9	13.4	19.4	48.4	32.2	—	2.10
								Mean for swath-combined				1.40
Straight-combined												
Before rain	18	88.9	5.6	5.6	11.5	17.3	13.1	94.4	—	5.6	—	1.11
After 1 rain	11	63.6	36.4	—	12.5	15.0	14.1	100.0	—	—	—	1.00
After 2 or more rains	17	70.6	23.5	5.9	11.3	18.4	13.5	58.8	29.4	11.8	—	1.50
								Mean for straight-combined				1.23

The group representing those collected after one rain is too small to give reliable results, but it is evident, in the straight-combined samples, that this exposure to rain had the general effect of increasing the number of No. 1 Northern samples at the expense of the No. 1 Hard group.

The exposure to two or more rains shows this tendency still more and in this group only 9% of the combined samples graded No. 1 Hard, as compared with 32% for the first group. Forty per cent of them graded No. 2 Northern as compared with 13% in the "before rain" group. The stook samples exhibit this tendency to a much lesser extent. The swathed samples, after two rains, showed a sharp decrease in percentage of No. 1 Hard and No. 1 Northern grades, with a corresponding increase in No. 2 Northern and the rejected grades, 24% falling into the latter category. This is owing to sprouting and moulding which occurred when the cut grain had been beaten down too close to the ground by rain. The rains during the collection period were not of sufficient extent or duration to effect any of this type of damage to either stooked or standing grain. These data merely confirm the general observation that grain in the swath is more susceptible to damage by moderate rain than grain in any other condition.

The change in value, from the grade standpoint, can be seen more readily by computing a sort of mean or average grade for the various methods and periods. In calculating such a figure it was necessary to assign arbitrary numerical values to the inspector's grades. For example, in the instance of common wheat, the values assigned to No. 1 Hard, Nos. 1, 2, 3 and 4 Northern, No. 5, No. 1 Northern rejected, No. 2 Northern rejected, No. 3 Northern rejected and No. 4 Northern rejected were 0, 1, 2, 3, 4, 5, 3, 4, 5, and 6, respectively. That is, the rejected grades were all dropped two units, which corresponds roughly to the average price discount.

The average grades calculated on this basis show that, while samples by all methods graded lower after two or more rains, the lowering was least in the stook and most in the swath, with the standing grain occupying an intermediate position. Considering all samples by the various methods, grouped without reference to period of collection, as in Table VIII, the average grades for stook, straight-combine and swathed samples are 1.04, 1.35 and 1.40, respectively. If these samples can be considered representative of the season's crop, it may be concluded that with both the straight-combine and the swathed combine, the average loss due to grade lowering compared to stook threshed grain, could be represented by a value equivalent to one third of the spread between No. 1 Northern and No. 2 Northern.

The durum wheat samples which were collected only in Manitoba showed somewhat different results. As can be seen from Table IX, the effect of exposure to two or more rains was about the same on both stook and straight-combine samples, and the general grade average for each of these classes is practically the same, being 1.25 and 1.23, respectively. The swath samples showed evidence of heavier grade damage even after exposure to one rain, the loss being about one grade. While the weighted mean given in the table

shows a value of 1.40 for average grade of all the swath-combined samples, the disproportion in numbers collected before rain and after two or more rains, doubtless biases this value toward the lower side. However, it may be concluded that the stook and straight-combine samples lost the equivalent of one-half grade, while the swath samples lost about one full grade as a result of exposure to several rains.

Summarizing the grade study, we may state that the stook-threshed samples showed least damage from rains, the swath-combine samples most, and on the whole the straight-combined samples were intermediate between these two.

Conclusion

The moisture and grade survey conducted in the 1932 harvest period has been very enlightening, inasmuch as, in a season as favorable as this, when practically all grain, no matter how harvested, was going forward as straight grade, it was found that 25% of the 416 samples of straight-combined wheat were actually tough or damp. This condition existed despite the fact that most of the factors complicating the harvesting of grain by this method were practically absent, when the bulk of the grain was being cut. Reference is made particularly to green weeds, uneven ripening and protracted rainy weather. Most of the fault in the season under study must, therefore, be attributed to the judgment of the operators. It appears reasonable to expect that in an unfavorable season, the percentage of tough and damp samples would be much larger.

NOTES ON THE BIOLOGY OF CERTAIN TORTRICID SPECIES WITH STRUCTURAL DETAILS OF THE LARVAE AND PUPAE[1]

By J. McDunnough[2]

Abstract

Biological notes are given on six species of Tortricidae—*Sparganothis directana* Wlk.; *Tortrix alleniana* Fern.; *Cacoecia myricana* McD.; *Cacoecia parallela* Rob.; *Tortricodes horariana* Wlshm. and *Peronea cornana* McD.: three species of Eucosminae—*Epinotia lindana* Fern.; *Epinotia myricana* McD. and *Anchylopera semiovana* Zell.: five species of Argyroplocinae—*Exartema cornanum* Heinr.; *Exartema permundanum* Clem.; *Exartema valdanum* McD.; *Argyroploce albiciliana* Fern. and *Evora hemidesma* Zell.

A comparative study of the setal pattern of both head and abdomen in the larvae of the above-mentioned species is presented and the main structural details of the pupae are also described. In this connection a critical comment on both Fracker's and Mosher's generic keys, based respectively on larval and pupal characters, is offered.

In the course of breeding work carried on in the Bobcaygeon region in Ontario during the summers of 1931 and 1932 the writer accumulated in alcohol a small collection of definitely associated and determined larvae of Tortricid species (in the broad sense), belonging to a number of scattered genera. Several of these fall into the family Tortricidae, the others into the subfamilies Argyroplocinae (Olethreutinae) and Eucosminae of the Eucosmidae, as treated by Heinrich (9, 10). As the life histories and food plants of the above-mentioned species are for the most part unknown, the writer offers in the present paper some biological details taken from field notes, and supplements these with structural studies of the individual larvae, these studies being largely based on the keys given in the Tortricid section of Fracker's paper (7) on the Classification of Lepidopterous Larvae, which has been reprinted by Forbes (6, p. 385) with certain generic changes.

With very limited material for study at his disposal Fracker was unable to offer at the time either subfamily or generic keys which would bring a larval classification into line with the system of classification then in use and based on adult characters; this system, as far as the Eucosmidae are concerned, has been since considerably altered by Heinrich's revision and the generic concepts in many instances radically changed. The present material has, of course, been far too scanty to do more than act as a sort of check on Fracker's work and the characters used for generic separation; in the main these characters have been found reliable, but in some cases where the generic value was doubtful this has been indicated under the individual species.

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A few brief notes on the various pupae have been appended, but a detailed study of them has not been made and will have to be left for a future occasion. The writer has confined himself mainly to enumerating structural points which are contradictory to the keys given by Mosher (12).

A great deal more work on the individual species will have to be done before any really satisfactory generic keys can be tabulated, but, as Fracker states, the larvae are of sufficient economic importance to warrant the expenditure of considerable time in such study, and the writer hopes to continue work along similar lines as occasion permits.

Tortricidae

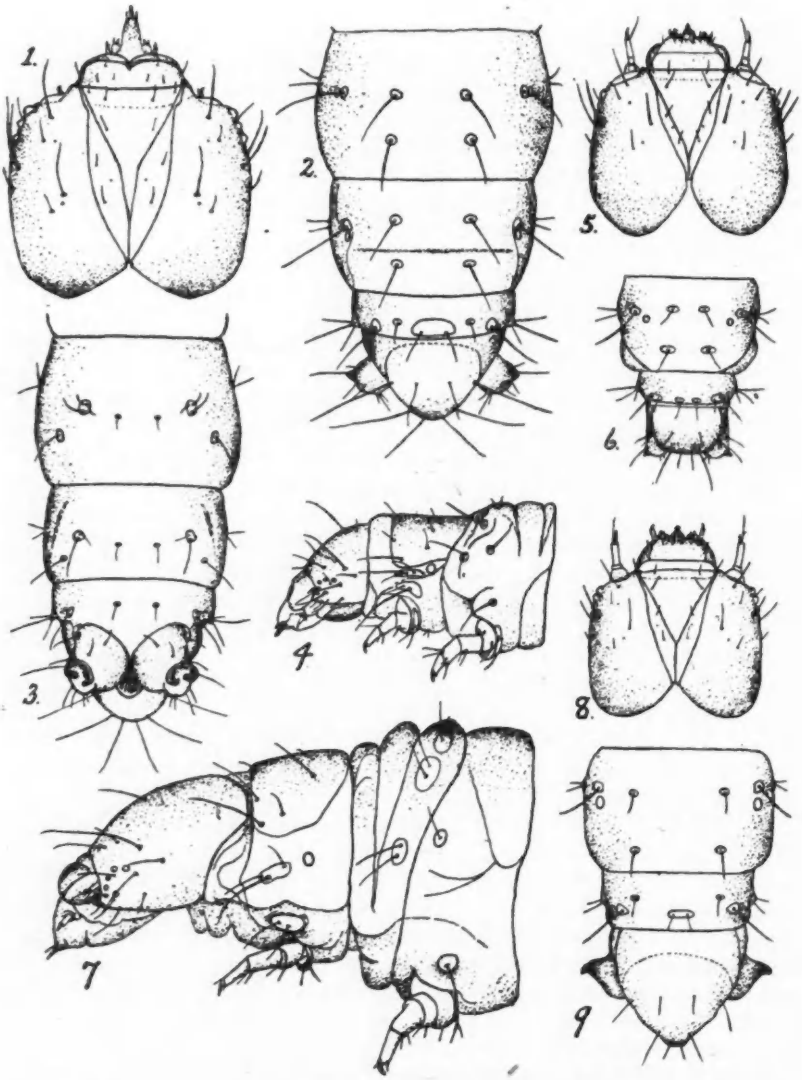
Sparganothis (Cenopis) directana Wlk.

This species has been classified in current check lists as synonymous with *reticulatana* Clem. Dr. Dyar, however, as early as 1902 (2, p. 402) maintained that it was a distinct species and recorded the larva on wild cherry in Colorado; Fracker probably examined these very larvae as he records *Cenopis directana* (7, p. 74) as one of the species studied.

The writer believes that Dr. Dyar was entirely correct in the above procedure, and Mr. A. Busck, with whom the writer has been in correspondence, confirms this determination. From a number of larvae found tying the terminal leaves of *Prunus virginiana* a series of moths was bred in late June, the males of which correspond quite closely to Walsingham's figure of the type of *directana* (14, p. 17); they show the same golden-yellow color on the primaries but the writer's specimens do not possess the complete, oblique, purplish median band shown in the figure, this being broken up into costal and dorsal spots, a variation frequently found in the entire group. The females have much darker forewings than the males with the purple-brown costal patches obsolescent; the light red-brown color of the secondaries in both sexes is quite characteristic.

Mature larvae have the head, prothoracic shield, pinacula of the prothorax and the legs deep blackish, the latter with the two terminal joints shading into paler brown. The mouth parts project rather strongly beyond the margin of the head capsule but the antennae are quite short (partly due to retraction in the material, in the writer's opinion). The body is entirely dark greenish dorsally as far laterad as the spiracular area and very faintly and finely shagreened; laterally and ventrally the color is a pale dull green, paler in color than the surrounding area; the pinacula are dull whitish but not strongly contrasting. The anal plate is conical, with convex basal margin, the anal fork is well developed and six- to eight-pronged.

As typifying the true Tortricids Figs. 1–4 are given showing the arrangement of the setae on head, thorax and abdomen. Particular attention should be given the characteristic position of *alpha*, *beta* and *rho* on abdominal segment IX, for in dealing with subsequent species attention will be merely called to any divergences from the figured arrangement shown here. A study of the figures will show that *directana* fits in excellently with Fracker's



FIGS. 1-4. *Sparganothis (Cenopis) directana Wlk.* FIG. 1. *Head (viewed dorsally).* FIG. 2. *Abdominal segments VII-X (viewed dorsally).* FIG. 3. *Abdominal segments VII-X (viewed ventrally).* FIG. 4. *Head and first two thoracic segments (viewed laterally).* FIGS. 5-7. *Epinotia lindana Fern.* FIG. 5. *Head (viewed dorsally).* FIG. 6. *Abdominal segments VIII-X (viewed dorsally).* FIG. 7. *Head and first two thoracic segments (viewed laterally and much enlarged).* FIGS. 8 AND 9. *Exartema cornanum Heinr.* FIG. 8. *Head (viewed dorsally).* FIG. 9. *Abdominal segments VIII-X (viewed dorsally).*

keys (7, p. 73) if we omit his captions *d* and *dd*. The position of the middle seta of the *Kappa* group on the prothorax in relation to the other two hardly bears out Fracker's contention that it is three times as far from the caudal seta as from the cephalic one; to the writer it appears to be only very slightly more than twice as far.

The pupa is rather dark brown; dorsally abdominal segments II–VIII show both rows of transverse blackish spines, although the caudal row on segment VIII is much reduced; there are no spines on IX or X. The cremaster is well developed, longer than broad, with four terminal and two lateral setae, making eight in all. There is a single laterocaudal seta on the anal rise, a feature which rather upsets Mosher's keys to families. The front shows a broad raised dumb-bell shaped area with smooth upper surface, somewhat constricted opposite the antennal bases.

A single female pupa of *Sparganothis unifasciana* Clem. from a larva feeding in a terminal shoot of a *Solidago* sp. shows a number of divergent features. While the frontal elevation and the spining of the first eight abdominal segments are similar, there is a very strong caudal row of spines on segment IX. The cremaster is greatly reduced, being broader than long and with the setae reduced to very minute spines, of which two terminal ones are best detected. There is no seta on the anal rise.

Tortrix alleniana Fern.

This well-known species is recorded by Forbes (6, p. 492) as being a general feeder in the larval state, but the writer has met with no detailed account of the early stages apart from that of Venables (13).

A few mature larvae tying the terminal shoots of *Monarda fistulosa* in early June were secured and these produced adults (1 ♂, 2 ♀) on June 21, 28 and July 1. In the mature larva the head is pale ruddy, the epicrania faintly marbled laterally with light brown; the sides of the vertical triangle are broadly suffused with black-brown, this color extending forward along the adfrontal suture as far as the posterior seta and forming roughly a triangular patch; the posterior edge of the epicrania as far as the lateral tubercle is narrowly brown; a small spot anterior to the first posterodorsal seta, the region of the ocelli and the posterior margin of the clypeus are also dark brown. The antennae are short and the whole shape of the head and position of setae very similar to that of *directana* except that the posterior epicranial setae with their puncture form more nearly a straight oblique line, with the puncture closer to the second seta. The prothoracic plate is similar in color to the head with a large posterior dark brown median patch and a similarly colored, irregularly lunate, lateral patch. There is also a small brown spot on the prothoracic segment above and slightly posterior to the *Pi* group of setae. The legs are shaded outwardly with brown and have dark streaks anteriorly at their base. The entire dorsal surface of the abdomen is a dark, dirty green, the integument in this area being very finely shagreened and containing minute scattered rather regular-placed, pale lenticles, principally along the first transverse fold of each abdominal segment (close to anterior

margin) and in two groups of three or four above tubercle *rho* (III); the pinacula stand out strongly as pale circular areas; laterally the color is pale green, becoming deeper again on the ventral surface of all segments but the thoracic ones. The anal plate is pale, conical, broad at the convex base, the sides narrowing rather abruptly to a bluntly truncate apex; there is slight brown sprinkling, principally in the basal section. The anal fork is strongly developed with seven prongs, much as in *directana*. The spiracles are broadly oval, almost circular, brown, ringed with black. The setal arrangement appears to be exactly as in *directana*.

The deep black-brown pupa shows both rows of dorsal transverse spines on abdominal segments II–VIII, considerably reduced in size on II; deep transverse grooves are situated dorsally on anterior margins of II and III; there are no spines on IX and X nor setae on the anal rise. The cremaster is longer than broad with four terminal and two lateral setae. There is a slight raised anchor-shaped prominence on the front between the antennal bases.

Cacoecia myricana McD.

Larvae of this species were not very numerous but about eight specimens were taken on *Myrica* where they live in a sort of tube formed by joining several leaves loosely together; three larvae were also secured from an alder bush, growing alongside the *Myrica* which, on a superficial examination, could not be differentiated from the *Myrica* feeders. From the *Myrica* larvae the writer reared three males and three females, these adults emerging June 20–24; the three males agree quite well with the author's original type series from Algonquin Park, Ont.; two of the females also agree with the type females in having more or less unicolorous red-brown primaries with little evidence of maculation; the third female, however, is much paler and very similar to females of *eleagnana* McD. The single male bred from the alder feeders is more sepia-brown, rather than ruddy brown, in the color of the forewings and approaches therefore close to *mortuana* Kft. Finally from a mixed lot of unsorted larvae on *Myrica* the writer bred a single large female of typical *argyrospila*. The above results, it must be admitted, are not very satisfactory in determining the status of the various forms of the *argyrospila* group; either the larval series was mixed, owing to lack of equipment in the field to enable the detection of small differences, or else (what seems quite probable) we are dealing in the case of the *Myrica* feeders with a form which has not yet entirely established itself as distinct from typical *argyrospila*, but is certainly working in that direction. Breeding from eggs of a known female should clear up the situation to a certain extent.

The full-grown larva of the *Myrica* feeder (the only form of which material was brought back in alcohol for study) can apparently be distinguished from *argyrospila* larvae, as represented by material from Vineland, Ont. It has a pale reddish head with the labrum, mandibles, frontal sutures, patch around the ocelli, posterior edge of epicrania, and a lateral longitudinal stripe extending backwards from between the second and third ocellar setae, deep brownish; the posterodorsal portions of the epicrania are quite heavily marbled

with pale brown, leaving a broad vertical stripe of the ground color extending to posterior margin and containing the posterior epicranial setae. The epicranial lobes are rather more rounded laterally than in *directana* and the pale antennae are slightly longer, although still quite short. The most noticeable feature in the arrangement of the setae as compared with the figure of *directana* is that the two posterior epicranial ones with the almost equidistant puncture form a straight, only very slightly oblique, line; the lateral epicranial seta is less obliquely situated with regard to the third anterior one, the width between them is relatively greater and both are situated farther behind the ocelli than is the case in *directana*. The grouping of the ocelli seems to be practically similar and the writer cannot detect that the second ocellus is farther from the first than from the third one.

The prothoracic plate is pale with a small brown patch in the anterolateral corner and a faint brown lunate mark dorsad of tubercle *rho*. Dorsally the entire body is deep olive-green, paling into dirty whitish laterally; there are distinct traces of pale subdorsal longitudinal bands crossing the region of tubercles *alpha* and *beta* and particularly evident on the anterior portion of the abdominal segments. The pinacula are pale but not very contrastingly so and the spiracles are dull brownish with a distinct dark outer ring. The legs are deep brown at the base paling into light brownish on the two terminal segments. The anal plate is pale and very similar in shape to that of *directana;* it is sprinkled with small brown lenticles on the basal section; such lenticles occur very sparsely also on the abdominal segments, in sections similar to those of *alleniana*, but are not nearly as prominent as in this species. The anal fork is seven pronged, much as in *directana*, and the arrangement of abdominal setae is also similar to that of this species.

In comparison a typical *argyrospila* larva has a black-brown head and the entire lateral edge of the prothoracic plate is rather broadly suffused with brown. The body is pale green and shows none of the deep olive-green dorsal shading found in *myricana*. It is true that Dr. Dyar (2, p. 400) maintains that there is a great variability in color for the heads of *argyrospila* larvae, but this needs further proof before it can be accepted; it is possible that either Dr. Dyar had his series mixed or that he made his observations on larvae immediately after a skin-shedding when the pigmentation had not developed. On the other hand his description of the larva of *vividana*, which he considers to be merely a variety of *argyrospila*, would fit in quite well for typical *argyrospila*. Both Venables (13) and Criddle (1) note that the heads of *argyrospila* larvae are blackish.

The pupa is deep blackish-brown and seems considerably darker in color than that of a female *argyrospila* bred from *Viburnum* and also from a male pupa of the same species, bred from birch. The writer cannot, however, detect any structural differences. There is the usual double row of transverse spines dorsally on abdominal segments II–VIII, the cephalic row on II being greatly reduced; on IX and X there are no spines in the female and only a few minute spines on IX in the male. On the anterior margins of II and III

are two deep subdorsal pits, separated from each other by a narrow mediodorsal ridge. There are no setae on the anal rise. The cremaster is longer than broad with four apical and two lateral setae. The front is not raised above the level of the antennal bases.

Cacoecia parallela Rob.

A few of the very striking larvae of this species were taken on *Myrica* along with those of *myricana*, the adults emerging at about the same time. With its reddish head and dark abdomen on which the white pinacula show up very distinctly, the larva is readily distinguished from other Tortricids feeding on the same plant.

The larva was briefly described by Edwards and Elliot (4, p. 80) and a rather full description was given by Fletcher (5), and further mentioned by Gibson and Ross (8, p. 18). The writer's observations correspond with those of the above authors and make it evident that the larva mentioned under this name by Washburn (15, p. 170) cannot have been correctly identified.

The head of a mature larva is light reddish with the mouth parts, antennae, a patch around the ocelli, a posterolateral longitudinal stripe on a level with the ocellar patch, the frontal sutures and posterior margin of epicrania, deep black-brown. There is some faint lateral light brown marbling on the epicrania and a trace of a dark streak on the lobes along the posterior section of the adfrontal suture. The shape of the head and the arrangement of the setae are practically as in *myricana*. The prothoracic plate is similar in color to the head with a broad black-brown border and a similarly colored anteromedian patch; the prothoracic pinacula and the legs are also black-brown.

With the exception of the lateral portion of the prothorax which is paler, the entire body is blackish-olive, the skin very finely shagreened and the white pinacula standing out very markedly from the dark body-color. There are scattered lenticles over the body surface as in *Tortrix alleniana* but not so prominent. The spiracles are pale brownish, ringed with black. The anal plate is somewhat paler than the body color and rather more bluntly conical than in *directana*, being almost as broad at its widest part as it is long. The anal fork is strongly developed, with six prongs. The setal arrangement of thorax and abdomen does not differ from that of *directana*.

Fracker includes this species in a section in which the *Pi* group on the meso- and metathorax is bisetose; the writer's material does not show this, on both segments the group being normal and unisetose.

The pupa is black-brown with the usual two transverse rows of dorsal spines on abdominal segments II–VIII, both rows somewhat reduced in size on II, the caudal row on VIII composed of very small spines in the male and both rows reduced in the female; a few minute spines on IX in the male and none in the female; no spines on X in either sex nor any setae on anal rise. Cremaster much longer than broad with four terminal and two lateral setae. Fairly deep transverse furrows on anterior dorsal margin of II and III. Front with strongly raised broad, transverse ridge between the antennal

bases, connected by a narrow ridge with a raised, inverted-U mark on the caudal section of the front. A very similar structure occurs in the pupa of *C. rosaceana* Harris, but in this species is less prominent.

Tortricodes horariana Wlshm.

Larvae of this species were not uncommon on wild gooseberry; they live singly, spinning up the terminal leaves into a small white web, somewhat like that of a Phycitid. They mature during early July and spin a tough, boat-shaped cocoon on the stalk of the plant, pupating within 10 days; emergence does not, however, take place until early fall, the dates on the writer's specimens ranging from September 20 to October 3.

The larva is entirely pale green. The head is rather flattened dorsally, almost as broad as long, with a distinct frontal suture, but with the adfrontal sutures scarcely distinguishable; the labrum is light brownish in color (alcohol specimen), not particularly large or prominent; the antennae are quite long and extend when fully drawn out to a level with the apex of the maxillary palpi. Setal pattern and other details much as in *directana;* the lateral epicranial seta (viewed from the side) is less obliquely situated with regard to the third anterior one and is more as in *Cacoecia myricana.*

Abdomen rather wrinkled, with large but improminent pinacula, due to the similarity in color to that of the abdomen; anal plate smooth, rather more than hemispherical, broadly rounded apically; anal fork well developed, five pronged. Spiracles small, pale, almost circular. Crotchets of prolegs biordinal. According to Fracker's generic key (7) the species would trace down to the same group as *Tortrix* and *Cenopis*, if we disregard his caption *d* which calls for the middle seta of the trisetose *Kappa* group on the prothorax to be three times as far from the caudal seta as from the cephalic one, in contrast to *dd* where the distance is only twice as far. In the present instance the distance is barely twice as far, but the writer has already commented on the fact that the character is probably an unstable one.

The pupa is light brown with rather short thick abdomen. The dorsal portion of each abdominal segment II–VIII is strongly rugulose as far back as the caudal row of spines, the remaining posterior sections being covered by a very fine network. The transverse rows of spines are greatly reduced and scarcely visible above the general surface rugosity, particularly the caudal row. The segments IX and X are smooth dorsally, without spines. The cremaster is short, much broader than long and bent sharply dorsad, almost at right angles; its terminal edge is provided with four equidistant spines, two median and two lateral with a fine seta midway between each outer pair; there is also a single lateral seta and a small one dorsally near the base. The anal rise is improminent and without setae. The front is smooth.

Peronea cornana McD.

Larvae of this species were very plentiful in June in laterally rolled leaves of *Cornus paniculata* and allied dogwoods. Superficially these tubular rolls are very similar to those of *Exartema cornanum* but on opening them the

larva is found to live in a silken tube; further, the frass is not ejected, but accumulates within the rolled leaf. Pupation takes place loosely within the roll, generally in, or close to, the latest fold.

The very active larva has a rather flat pale reddish head with the mouth parts shaded with brown and the antennae moderately long; a patch around the ocelli and a posterolateral streak on the same level, deep black-brown. The setal arrangement is much as in *directana* except that the posterior epicranial setae with their equidistant puncture form almost a straight, somewhat oblique line.

Entire body, including the legs and prothoracic plate, pale green with at times a brownish shade along the anterior margin of the prothoracic plate; pinacula pale, not well defined; anal plate with rather broadly rounded apex, more hemispherical than conical, with the basal edge not distinctly defined; anal fork well developed, five- to six-pronged, spiracles pale, whitish. On the ninth abdominal segment seta *alpha* is situated considerably more forward of the line between *beta* and *rho* than is the case in *directana*, and the *Pi* group is bisetose on both segment VII and segment VIII and occasionally unisetose on IX; this character is given generic value by Fracker. Judging by the present species, Forbes' figure (6) of the setal arrangement of a *Peronea* sp. is inaccurate as far as the ninth abdominal segment is concerned; the *beta* setae are shown as separate instead of on a single pinaculum, *alpha* is too close to *rho* and the *Kappa* group should be on a single pinaculum (as in his Fig. 245) instead of being represented as separate.

The light brown pupa corresponds excellently with the characterization given by Mosher for the genus *Peronea*.

Eucosminae

Epinotia lindana Fern.

Dr. Dyar commented briefly on the larva of this species (3, p. 928) giving the food plant as *Cornus*.

In the early spring the writer found the larvae very plentiful, tying the young terminal leaves of *Cornus paniculata* and allied species; as noted by Dr. Dyar the leaves so tied were mostly killed and formed an unsightly bunch among the fresh green foliage. The sluggish grub-like larva was generally found in the centre of the mass in a fold of a dried leaf. Under natural conditions the larvae apparently leave the plant when ready for pupation about the middle of June and spin a rather firm cocoon under rubbish on the ground; pupation does not actually take place for a month or six weeks, the larva remaining unchanged in its cocoon until August. The actual pupal period lasts about two to three weeks, the moths emerging at the end of August and during September.

The larva is dull whitish or dirty greenish with the head, prothoracic plate, pinaculum of the *Kappa* group on the prothorax and the legs, brown. In mature larvae the anterior portion of the prothoracic plate is shaded with paler color; on the head the labrum, patch around the ocelli, frontal sutures

and rear margins of epicranial lobes are deep black-brown. The setal arrangement of the head is shown in Fig. 5 and it should be noted that the posterior epicranial setae have moved forward considerably as compared with those of the true Tortricids (see *Sparganothis directana*, Fig. 1); also that the position of the anterior epicranial puncture (as far as can be ascertained, it being very difficult to locate in this species) is *posterior* to both its setae. On the prothorax setae *gamma*, *eta* and *rho* form more or less of an equilateral triangle and in the *Kappa* group the middle seta is situated ventrad of a line between the other two; on the other thoracic segments and on the first seven abdominal segments the position of the setae is normal, except that on VII the *Pi* group is bisetose (not trisetose as on preceding segments) and remains so on the following two segments. On segment VIII the spiracle has moved up well dorsad of *rho* and on IX *alpha* is associated with *rho* on a single pinaculum, and the three setae of the *Kappa* group in a vertical row on one pinaculum. The spiracles are pale with brown ring; abdominal pinacula large but improminent, anal plate hemispherical, occupying almost the entire dorsum; anal fork weak, consisting of three or four short prongs; hooks of prolegs biordinal, forming a complete circle. By Fracker's key (7) the species would trace to the genus *Eucosma*.

The pupa is light brown. On segments II–VII there are double transverse rows of dorsal spines, the caudal row consisting of much smaller spines than the cephalic one; on segments VIII–X only the cephalic row is present, those on X being larger than on IX and arranged in a semicircle around the slightly raised, blunt, caudal end. The cremaster is lacking, but there is a dorsolateral and a ventrolateral seta on each side of the caudal end and a lateral seta arising from a distinct papilla on the anal rise. There are no furrows or pits on the abdominal segments. The front shows a small conical rise. The pupa does not fit in at all with Mosher's keys (12) to the genus *Epinotia* (based on *saliciana* Clem. and *piceafoliana* Kft., only the latter species being now included in the genus) but falls rather to *Enarmonia* (based on *fana* Kft., a species now placed in *Grapholitha*).

Epinotia myricana McD.

The larvae of this species were not uncommon on *Myrica;* as in the preceding species they are rather sluggish and grub-like. They mature early in June and in the breeding tins spun a rather firm cocoon under paper or refuse, pupating in from 10 days to two weeks; the pupal stage lasts approximately a month, the moths emerging singly and irregularly during the last three weeks of July.

The larva is dirty white with the entire dorsal area suffused with dull greenish and very finely shagreened, the rather large pinacula remaining pale. The head is pale greenish white with considerable brownish marbling on the epicranial lobes posteriorly and laterally; the labrum, a patch around the ocelli, the frontal sutures and the posterior margin of the lobes deep black-brown. The setal arrangement shows the following differences from that of *lindana:* the posterior adfrontal seta has moved forward in about a line

with the first posterior epicranial one, the two adfrontal setae in consequence being very close together; the anterior epicranial suture has moved forward slightly to the same level as the second anterior seta.

The prothoracic plate is pale with sparse brown sprinkling; the setal arrangement of the prothorax is much as in *lindana* but in the *Kappa* group the middle seta is almost in alignment with the other two and only slightly nearer to the cephalic seta than to the caudal one. On the other thoracic segments the *Pi* group may be bisetose; a larva has been examined which is bisetose on one side and trisetose on the other, so that the lack of a seta has evidently no classificatory value. On abdominal segment VII the *Pi* group may be either bisetose or trisetose; on VIII the spiracle is hardly as far dorsad as in *lindana;* on IX the arrangement is practically identical, the pinacula of the two *beta* setae and of *alpha* and *rho* being normally fused. Anal plate pale, hemispherical as in *lindana;* anal fork much stronger than in *lindana*, composed of seven prongs. Spiracles pale, black ringed, with a faint brownish surrounding shade.

The brown pupa is almost identical structurally with that of the preceding species, except that in some cases there are two further fine setae situated at the caudal end nearer the median line, besides the four already noted; this, however, is by no means a constant feature. The pupa of *E. solandriana* Linn. also agrees in structural details with the present two species, showing distinctly in the one specimen examined (bred from larva on birch at Bobcaygeon, July 6) the six terminal setae.

Anchylopera semiovana Zell.

In both 1931 and 1932 the moths of this species were extremely abundant during the latter half of June and early July around bushes of *Ceanothus americana* from which they were readily beaten. In spite of repeated searching no trace of possible larvae could be found until early August, 1932, when very small larvae were taken on *Ceanothus*, living either in a slight fold at the edge of a leaf or in a longitudinal fold along one of the ribs. These were brought back to Ottawa and, by forcing, a partial second and rather undersized generation of the present species was secured in September; under normal conditions it seems likely that, in Canada at least, the larva hibernates nearly full grown.

The larva is light yellow-green with rather prominent pale pinacula on the abdomen, and a well-defined division of each segment into two obliquely semiequal subsegments, the posterior one of which may again be subdivided into dorsal and lateral portions. The head and both prothoracic and anal plates are paler than the dorsum of the abdomen; the former has the mandibles light brown, a deep black-brown area around the ocelli and a small posterolateral blackish spot on a level with the ocelli; the prothoracic plate has a prominent round blackish spot in the posterolateral angle and the anal plate is crossed just posterior to the first row of setae, by a lunate dark brown band. Anal fork well developed, six pronged; legs pale; spiracles pale with black ring.

Notwithstanding the fact that Heinrich (9, p. 243) in his revision derives the genus direct from *Epinotia*, the larva of the present species, by the arrangement of both its head setae and those of the ninth segment, shows far closer relationship to the true Tortricids than to *Epinotia* and in this respect Fracker's reference of the genus to a group with *Tortrix* and *Cenopis* is confirmed. The setal arrangement on IX is as in the writer's figure of *directana* except that the *alpha* pinaculum has moved somewhat more cephalad; the same similarity exists between the ventral setae on the posterior segments; the anal plate has the posterior margin less evenly rounded than in *Epinotia lindana* and a tendency to be somewhat conical. On the prothorax the middle seta of the *Kappa* group is ventrad of a line between the other two and about twice as far from the posterior one as from the cephalic one; on the head the arrangement is much as in *directana* except that the anterior epicranial puncture is closer to A_2 than to A_1.

The pale brown pupa corresponds in all respects with Mosher's characterization of the genus *Ancylis*.

Argyroplocinae (Oleuthreutinae)

Exartema cornanum Heinr.

The larvae were obtained quite readily in tightly, laterally rolled leaves of dogwood (*Cornus* spp.) in early June; these spiral rolls are quite similar to those of *Peronea cornana* outwardly, but differ when opened out in that the larva does not live in a silken tube and that all frass is ejected from the roll and not left inside it, as is the case with *Peronea*. The larva pupates within the tube, turning down the edge of the leaf to form a compact cocoon; the pupa is readily secured by hunting for the characteristic spiral leaf-rolls in late June, although it is often found that at this time either birds have picked open the roll and obtained the pupa or that *Macrocentrus* cocoons have taken its place.

The larva is pale green with light reddish head and prothoracic plate; on the head a patch around the ocelli and a posterolateral streak on the same level as the ocelli are black-brown; the pinacula are moderate in size and somewhat paler than the ground color; the anal plate is conical. The position of the setae on the head capsule (Fig. 8) seems closer to that occurring in the Tortricids, especially in species of the genus *Cacoecia*, than to *Epinotia;* the frontal sutures, however, are perfectly V-shaped and not concave in the dorsal third which neither agrees with the figure of *Sparganothis* nor with Fracker's key. Nothing specially different in the setal arrangement on the thoracic and first eight abdominal segments can be found; the three setae of the *Kappa* group on the prothorax are in alignment; on all abdominal segments *kappa* and *eta* are almost vertically placed, *eta* being very slightly caudad of *kappa*. On segment IX seta *alpha* is closer to *rho* than to *beta* (see figure) but not on a single pinaculum with it and well anterior to both it and *beta; mu* is on the same pinaculum with *kappa* and *eta* and situated very slightly caudad of the other two which are placed vertically. The anal plate is typically Tortricid and the anal fork well developed, with seven prongs.

The dark brown pupa runs to *Exartema* (a) in Mosher's keys; it has a strong frontal prow, which, viewed dorsally, is tongue-shaped and from the side roughly triangular.

It might be noted that larvae of *Exartema punctanum* Wlshm, were taken along with those of *cornanum* but not differentiated from them; the very similar pupa, however, was found to have apparently a decidedly paler brown color on the wing sheaths in *punctanum* (deep brown in *cornanum*) and to emerge, on the whole, a week or two later. Most of the writer's material of this species was collected as pupae from the spirally rolled leaves.

Exartema permundanum Clem. (?)

From larvae obtained on *Myrica* in June, along with those of *Cacoecia myricana*, *C. parallela* and *Epinotia myricana*, adults were bred which appear to belong to a dark form of this species. On the primaries the dark areas are either partly or entirely covered with ruddy scaling which seems to be entirely lacking in the typical form (as determined by C. Heinrich based on Clemens' type specimen) in which these areas are olivaceous over a brown base; the secondaries too in both sexes are deeper black than in typical *permundanum*. There are no tangible differences in either the male or female genitalia and until more definite information is available regarding the larva of the typical form and its food plants, as well as of the variety *gaylussacianum* (a Kearfott Mss. name which was validated by Heinrich in his revision, page 155, for the huckleberry feeder), it scarcely appears advisable to name the present form.

The larva is light green with black head and prothoracic shield and some blackish shading on the prothoracic pinacula and on the legs, notably those of the prothorax. The skin, under a moderate magnification appears finely but definitely shagreened. The general structure and setal arrangement is much as in the preceding species; on the head, however, the frontal sutures are more definitely concave in the dorsal third and the species, therefore, fits in better with Fracker's key; in the arrangement of the ocelli the second is somewhat closer to the third than to the first. The anal plate is more bluntly conical, the apex of same being broader than in *cornanum;* the anal fork is well developed with six rather long prongs of a darkish color. The pupa is without the cephalic prow of *cornanum* and very similar to that of the following species. The larvae of this and of the following species are extremely difficult to differentiate from half-grown larvae of *Cacoecia rosaceana* Harr. which occur on the same food plants. The closer association of *alpha* with *rho* on the ninth segment in the *Exartema* species is generally helpful in distinguishing the species, but the writer has noted that in a certain proportion of *rosaceana* larvae, *alpha* is certainly somewhat closer to *rho* than to *beta*, although normally equidistant. An additional point of distinction is that the anal plate in *rosaceana* is much less conical with an almost rounded apical margin. Mature larvae of *rosaceana* are naturally much larger and show a marked tendency for the head and prothoracic plate to become either partly or entirely pale brown.

Exartema valdanum McD.

A small series of this species was bred from larvae obtained on *Spiraea salicifolia* in June along with those of *Evora hemidesma* Zell. and *Argyroploce albiciliana*, all of these species tying the terminal leaves of the plant. Clemens in his original description of *permundanum* mentions *Spiraea* as the food plant of the species; it is, however, to judge by the description, quite probable that his series was mixed and that the bred specimen actually belonged to what we now know as *valdanum;* in any case 12 bred specimens of the species described here all show very constantly the white antemedian band of the forewing which characterizes *valdanum.*

The very active larva is pale green with black head and prothoracic plate and some blackish suffusion on the prothoracic pinacula, especially the *Kappa* one, as well as on the legs, which are partly pale brown. It is very similar to the larva of the preceding species but shows the following slight points of difference: the skin is less evidently shagreened; on the ninth abdominal segment the *beta* setae are on separate pinacula (possibly not constant); the anal plate is slightly narrower at the apex and the prongs of the anal fork are shorter, weaker and paler in color.

Pupation occurs early in June and the light brown pupa is also without a prow; the slightly raised portion of the front being roughly dumb-bell shaped. It agrees in other respects with Mosher's characterization of the genus *Exartema* (a).

Argyroploce albiciliana Fern.

Apart from Heinrich's record of *Spiraea salicifoliana* as the food plant, based on Kearfott's notes*, the writer knows of no larval records of this species.

The rather sluggish, grub-like larvae were not uncommon tying the terminal shoots of the above-mentioned plant in June and are at once recognizable by their entirely blackish coloration. The head, legs and anal plate are shining black, remainder of body, including the prothoracic plate and abdominal pinacula, deep, dull black-brown very finely shagreened. While there appears to be nothing very different in the setal arrangement on the head from that of *Exartema cornanum*, there are a number of differences in the position of the body setae; in the three aligned setae of the *Kappa* group on the prothorax the middle seta is almost equidistant between the caudal and cephalic setae, being only slightly closer to the latter, instead of at least twice as close; on the first two and the seventh abdominal segments the *Pi* group is bisetose, and unisetose on the eighth and ninth segments; on the eighth abdominal segment the *beta* setae are already somewhat closer together than the *alpha* ones, whilst on the ninth segment they are extremely close to each other and *alpha* and *rho* are situated on a single pinaculum, the area of skin between the two *rho* pinacula being more lined and roughened than

*See Reference 10.

on the remainder of the segment. The anal plate is conical, rather more bluntly so than in the figure of *Exartema cornanum;* the anal fork is strong, consisting of four stout, blunt, blackish prongs.

The dark brown pupa has a well-developed cephalic prow, narrowly cylindrical with two apicolateral tubercles, the whole with considerable resemblance to the head of a Neuropterous insect; there is a further tubercle at the base of each antennal sheath. The cremaster is greatly reduced, being represented at the best by two small triangular lateral projections with the usual number of rather thin setae between them; there are two similar setae on each side of the anal rise and no spines dorsally on the tenth segment.

Evora hemidesma Zell.

The larva of this species is briefly recorded by Kearfott (11) as feeding on *Spiraea tormentosa*. The writer found them about equally common with the preceding species on *Spiraea salicifolia* in June. They are also blackish-brown in coloration of the abdomen but may be readily distinguished by the pale head, prothoracic and anal plates and by the pale yellowish abdominal pinacula.

The head is light yellow-brown, the area around the ocelli and a long posterolateral streak extending forward to the ocellar setae, as well as shading on the mouth parts, dark black-brown; the setal arrangement is much as in *Exartema*, except that the anterior epicranial puncture has moved cephalad to a position almost equidistant between the two setae. The prothoracic plate is colored similarly to the head with two large, irregular, posterolateral black-brown patches. The whole body is black-brown with the exception of the pale pinacula and is finely, but distinctly, shagreened; the legs are blackish. The setal arrangement shows no variation from that found in *Exartema* and differs, therefore, from the preceding species in this respect. The anal plate is pale yellowish with a dark, lunate band starting in the posterolateral corners and curving caudad of the first pair of setae; the anal fork is well developed with six palec-olored prongs.

The black-brown pupa is provided with a frontal prow very similar to that of *Exartema cornanum* as already described; in addition, however, there are tubercles at base of antennal sheaths, slightly smaller and blunter than in the preceding species. There is a short broad cremaster, the apical edge, viewed dorsally, showing two sharp lateral projections; in the medioventral area is a raised ridge, the whole cremaster being very similar to that of *Exartema*, with the usual number of four hooks, two apical and two lateral on each side of the median line. The anal rise is provided with two lateral setae on each side, much smaller than the cremastral hooks and there is a distinct group of spines dorsally on the tenth segment, arranged in several closely approximated rows.

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